CONSEQUENCES OF CHANGING BIODIVERSITY FOR PLANTS, INSECTS, AND ECOSYSTEMS

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Natural systems are challenged by invasions, extinctions, urbanization, and disturbance. Some species (or genotypes) persist despite these challenges, whereas others are lost. This dissertation asks [1] which species' attributes predict their ability to respond to environmental change, [2] how do changes in the composition of plant communities affect system functioning, and [3] can we use information about how species interact in diverse communities to inform the design of urban systems? Chapter 1 addresses the first question with an examination of plasticity among native and exotic congeners in response to altered competition and fertilization. We found that weedy exotics were not more plastic than natives, but instead that plasticity was more similar within genus. Chapter 2 and Chapter 3 explore how changes in diversity impact natural systems. Species richness is generally increasing due to the introduction of exotic species, and Chapter 2 asks how changes in exotic versus native plant diversity impact plant productivity and arthropod community structure. We found that diverse exotic communities were equally, if not more, productive than native communities and that they recruited an equally abundant and diverse arthropod fauna. However, exotics diminished the relative fruit production of co-occurring native species and recruited fewer arthropod species than natives. Chapter 3 provides the first direct comparison of how changes in genotypic diversity compare to changes in species diversity. We show that increasing either genotypic diversity of common

evening primrose (*Oenothera biennis*) or old-field species diversity resulted in nearly equivalent increases in aboveground primary production. Arthropod species richness also increased with both types of plant diversity. Finally, Chapter 4 integrates ecological principles from the biodiversity-ecosystem functioning literature into the design of vegetated rooftops. Most green roof plantings include only one or a few drought-tolerant species. We review the green roof and ecological literature to establish a clear research agenda for creating diverse and dynamic green roof ecosystems.

BIOGRAPHICAL SKETCH

Susan C. Cook-Patton (née Cook) grew up in the suburbs of Cincinnati, OH and Newcastle Upon Tyne, England. As a child she fell in love with the small wild places found in backyards, woodlots, and agricultural fields. Her interest in the intersection of people and nature continued throughout her undergraduate years, when she pursued a dual degree in the humanities and the sciences. After completing three majors at Indiana University in Biology, Psychology and English, Susan worked as a naturalist at the Aullwood Audubon Center and Farm. This experience confirmed her interest in the field of ecology and convinced her to work as a research associate with Dr. Keith Clay, studying the invasion of autumn olives into abandoned agricultural fields. Susan continued her investigations of the ecology of abandoned agricultural fields and highly altered natural environments during her PhD. From 2006 to 2012, Susan worked with Dr. Anurag Agrawal to study how changes in plant diversity through the invasion of non-native species and the extinction of native species (or genotypes) impacted plant-insect interactions and ecosystem functions.

To my grandmother, Marcella Bornhorst Mai, and all the other brilliant women who did not receive the opportunities to thrive intellectually as I did

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CHAPTER 1

RELATEDNESS PREDICTS PHENOTYPIC PLASTICITY IN PLANTS BETTER THAN WEEDINESS

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ABSTRACT

Background: Weedy non-native species have long been predicted to be more phenotypically plastic than native species.

Question: Are weedy non-native species more plastic than natives?

Organisms: Fourteen perennial plant species: *Acer platanoides, Acer saccharum, Bromus inermis, Bromus latiglumis*, *Celastrus orbiculatus, Celastrus scandens, Elymus repens, Elymus trachycaulus, Plantago major, Plantago rugelii, Rosa multiflora, Rosa palustris, Solanum dulcamara* and *S. carolinense*.

Field site: Mesic old-field in Dryden, NY (42º27'49" N, 76º26'19" W)

Methods: We grew seven pairs of native and non-native plant congeners in the field and tested their responses to reduced competition and fertilizer addition. We measured the plasticity of six traits related to growth and leaf palatability (total length, leaf dry mass, maximum relative growth rate, leaf toughness, trichome density, and specific leaf area).

Conclusions: Weedy non-native species did not differ consistently from natives in their phenotypic plasticity. Instead, relatedness was a better predictor of plasticity.

INTRODUCTION

Non-native species can negatively impact native ecosystems and are a source of concern for ecologists, land managers, and policy makers (Lodge et al. 2006; Vitousek et al. 1996). Biologist often try to identify traits of successful non-native species in order to understand the factors that have contributed to their success and to detect potential invaders before they become problematic (Lodge et al. 2006; Mack 1996). Phenotypic plasticity, which refers to an organism's ability to alter its

phenotype in response to the environment, has been implicated as a potential characteristic of "weeds" for almost 50 years (Baker 1965; Richards et al. 2006). Plasticity may aid in the establishment and spread of non-native species by allowing them to respond adaptively to the novel abiotic and biotic conditions in the introduced range (Bradshaw 1965; Schlichting & Levin 1986).

However, other plant characteristics may better predict variation in plasticity among species. One alternative hypothesis is that closely related species show more similar patterns of plasticity than distantly related species, regardless of non-native or invasive status (i.e., plasticity is evolutionarily conserved). Some evidence for this idea comes from Hoffmann and Franco (2003), who measured leaf trait plasticity in tropical forest and savanna species pairs, and found that genus explained up to 69% of the variation in plasticity among species. Another study by Kembel and Cahill (2005) combined data across 102 species from multiple families and found a strong signal of phylogenetic conservatism in how the species responded with root proliferation to soil nutrients patches (though not in other traits).

To address whether non-native weedy species are more plastic than native species, as well as account for variation in plasticity that is due to evolutionary history, we require comparisons of related species that differ in weediness. We conducted a field experiment using seven pairs of native and non-native congeners from six different plant families. We determined the plasticity of plants to four environments (a 2 x 2 factorial manipulation of competition and nutrients). We chose to manipulate competition and nutrients because successful non-native species are thought to respond strongly to human disturbance, which often reduces competition and increases nutrient availability in the environment (Davis et al. 2000; Hobbs & Huenneke 1992). We used congeneric pairs to minimize variation in the comparison of weedy non-natives and related natives (Agrawal et al. 2005) and because each congeneric pair

represents a phylogenetically-independent test of the hypothesis that non-native weeds are more plastic than natives.

METHODS

Species

We employed seven congeneric pairs (Table 1.1) of natives and non-natives (non-natives listed first in all cases): *Acer platanoides* and *A. saccharum* (Aceraceae), *Bromus inermis* and *B. latiglumis* (Poaceae), *Celastrus orbiculatus* and *C. scandens* (Celastraceae), *Elymus repens* and *E. trachycaulus* (Poaceae), *Plantago major* and *P. rugelii* (Plantaginaceae), *Rosa multiflora* and *R. palustris* (Roaceae), and *Solanum dulcamara* and *S. carolinense* (Solanaceae). All species occur in Tompkins County, New York (USA) where the experiment was conducted. Also, all the species can be found in old-fields or around field margins and thus grow in habitats similar to our experimental conditions.

Analyses of how plasticity facilitates the establishment and spread of non-native species can focus on either invasive/native or invasive/non-invasive non-native comparisons (Richards et al. 2006). The latter approach asks why some non-native species become invasive and others do not, and whether plasticity contributes to this difference (Richards et al. 2006). In contrast, we chose to test weedy non-native species against native species because we were interested in how differential plasticity impact plant performance in this primarily native plant community.

The species pairs were selected for several reasons. First, the congeners have similar habitats, morphologies and life histories (see Table 1.1), but are native to different continents. All the non-native species have been described as "invasive" in the scientific literature and are considered "noxious" species in the USDA Plants

Table 1.1 Species information for the 14 species employed. Under Origin, No = non-native and Na = native. Samples sizes in the four treatments are given for each species (no competition/no nutrient (••), competition only (C•), nutrient only (•F), and competition/nutrient (CF)).

Family	Species	Origin	Form	$N_{..}$	$N_{C\bullet}$	$N_{\bullet F}$	N_{CF}
Aceraceae	*Acer platanoides*	No	tree	16	22	17	19
	Acer saccharum	Na	tree	21	16	16	19
Celastraceae	*Celastrus orbiculatus*	No	vine	6	7	10	9
	Celastrus scadens	Na	vine	10	10	10	10
Poaceae	*Bromus inermis*	No	C3 grass	5	5	4	5
	Bromus latiglumis	Na	C3 grass	5	4	6	6
	Elymus repens	No	C3 grass	11	12	14	13
	Elymus trachycaulus	Na	C3 grass	15	14	14	13
Plantaginaceae	*Plantago major*	No	forb	12	9	11	4
	Plantago rugelli	Na	forb	14	14	16	14
Solanaceae	*Solanum dulcamara*	No	vine	16	15	15	16
	Solanum carolinense	Na	forb	15	15	15	15
Rosaceae	*Rosa multiflora*	No	shrub	4	5	6	4
	Rosa palustris	Na	shrub	3	3	3	4

Database (available on-line at http://plants.usda.gov/). However, the "invasive" moniker is becoming increasingly controversial (Brown & Sax 2004; Davis et al. 2011) so we have instead employed the terms non-native and weedy to describe the species studied here. There is some evidence that *Acer platanoides* (Reinhart 2003; Wyckoff & Webb 1996), *Bromus inermis* (Dillemuth et al. 2009; Otfinowski et al. 2007) and *Rosa multiflora* (Meiners et al. 2001) are highly invasive in that they can displace native vegetation. The remaining non-native species may be more appropriately called weedy because they grow vigorously and spread rapidly, particularly in disturbed environments, but it is unknown whether they displace native species (Dreyer et al. 1987; Hawthorn 1974; Moffatt et al. 2004; Palmer & Sagar 1963; Steward et al. 2003).

We mostly used field-collected seeds from Tompkins County (New York, USA) and southern Ontario (Canada) to establish our experimental plants. Seeds for woody species (*Celastrus, Acer* and *Rosa*) were surface-sterilized in 10% bleach for 10 minutes, sprayed with fungicide to prevent molding (Ortho Multi-Purpose Fungicide; Daconil 2787), and cold-stratified (4ºC) for 2.5 months to break dormancy. Non-woody seeds were cold-stratified for one week. All seeds germinated in moist petri dishes on a sunny windowsill.

In mid-May 2007, we sowed individual seedlings into 500 mL pots filled with potting soil (Pro-mix "BX" with biofungicide, Premier, Quakertown, PA) and grew the species in a hoop house. Seeds for three of the woody species did not germinate, including both *Acer* species and the native *Celastrus scandens*. To compensate, we collected naturally-germinated *Acer* seedlings at the cotyledon stage from beneath adult trees. We purchased *Celastrus scandens* seedlings from a nursery that specializes in local, native plants (Plantsmens Nursery, Groton, NY). These seedlings were planted in the hoop house with the other experimental seedlings.

Environments

Our field site was a mesic, abandoned agricultural field in Dryden, NY (42º27'49" N, 76º26'19" W) that was fenced to exclude deer. The resident vegetation in the entire field was initially and uniformly trimmed to a height of 0.25 m. This field was then divided into 0.75 m x 0.75 m plots (N = 612) and environmental manipulations were applied randomly to each individual plot. We used a 2 x 2 full factorial design such that some plots received no manipulation (control), some received either fertilizer or reduced competition, and others received both fertilizer and reduced competition.

To achieve "low-competition" treatments, we sprayed herbicide (2% glyphosate, Monsanto) to kill all vegetation two weeks before planting and maintained low competition throughout the experiment by clipping weeds at the soil surface (Figure 1.1). We did not uproot weeds to avoid additional soil disturbance. To achieve "high competition" plots we did not control the surrounding vegetation (Figure 1.1), because we wanted to employ a competitive environment that was more realistic and more closely matched conditions in which these species naturally grow. Although realism trades off with control, our treatments and plants were arrayed randomly throughout the field so we do not believe we introduced any bias due to differential growth of the naturally occurring vegetation. For "high nutrient" plots, we placed slow-release fertilizer (~16 g Osmocote Vegetable & Bedding Smart-Release Plant Food; 14:14:14 NPK, Scotts Company) at the base of each experimental seedling's root ball as it was planted. The "low nutrient" plots received no fertilizer. In June 2007, we planted a single individual plant in the middle of each plot. We assumed that mortality within the first two weeks was due to transplant stress and replaced dead seedlings with plants of equal age.

Figure 1.1 A photograph of two adjacent experimental plots, both containing an individual *Plantago* spp. On the left is a high competition plot and on the right, a reduced competition plot. Arrows indicate the experimental plant.

Replication

Replication depended on germination and survival rates, but was generally comparable within a genus (N = 612 plants in sum, see Table 1.1). *Rosa* and *Bromus* spp. had low replication, so we planted these species randomly with respect to treatment and species in a small block to minimize spatial variation. The remaining 12 species were arrayed randomly with respect to treatment and species in a much larger block that was directly adjacent to the *Bromus* and *Rosa* block. We ran the statistical analyses without *Rosa* and *Bromus* to determine whether the block effect qualitatively changed the results. As it did not, we included them with the rest of the data in the final analysis.

Traits

To assess phenotypic plasticity of the plants in the different environments, we measured six traits representing plant growth (maximum growth rate (RGRmax), total plant length, total leaf biomass, specific leaf area (SLA)) and palatability to herbivores (leaf toughness, and trichome density, SLA also affects palatability). Successful non-native species were predicted to respond strongly to the increased nutrient availability that results from increased soil fertility and reduced competition (Davis et al., 2000).

Changes in growth traits in response to the environmental manipulations should reflect this ability to capitalize on nutrient flushes. We were also interested in how leaf palatability traits would change in response to the environmental manipulations, as the success of non-natives has also been attributed partly to release from the natural enemies that regulate plant growth in the native range (Keane & Crawley, 2002). Enemy release may interact with resource availability to facilitate the spread of non-native plants in high nutrient environments can be more palatable/less defended and thus benefit more from enemy release (Blumenthal, 2006).

To measure RGRmax we calculated the changes in height (or in leaf length for *Plantago* spp.) that occurred between six sampling dates (planting date, 7/8/07, 7/17/07, 8/1/07, 8/27/07, harvest date), using the formula:

$$RGR_i = (ht_t\text{-}ht_{t-1} / ht) \times (1/days)$$

This resulted in five measures of RGR. In our statistical model, we used the highest measure (RGRmax) for each plant. Total plant length is a measure of the spread of a plant, either how much it branches or how broad its footprint is on the soil. For most plants, total length was the cumulative length of all branches on a plant, except for the grasses (*Elymus* spp. and *Bromus* spp.) where total length is equal to plant height and *Plantago* spp. where total length is the length of the longest leaf in each rosette. Total leaf biomass is a measure of primary productivity and plant performance. We collected leaf biomass in September – October, when plants had reached peak growth and species within each genus were always harvested at the same time. We dried the tissue in drying ovens (65°C, 4 days) before weighing it to the nearest 0.001 g. Toughness affects palatability to herbivores, indicates leaf structural investment and tends to decrease in shade or with fertilizer (Coley, 1983; Hemmi & Jormalainen, 2002). We assessed the toughness of the youngest fully formed leaf on each plant using a penetrometer (Type 516, Chatillon Corp. NY), which records the amount of force needed to puncture a leaf. Trichome density is involved in resistance to herbivores and water relations, where hairy leaves are less damaged and lose less water via evapotranspiration (Woodman & Fernandes, 1991). To measure trichome density, we took a 29.29 mm2 hole punch from the tip of the youngest fully expanded leaf, centered on the mid-vein and used a dissecting scope to count trichomes on the top and bottom of each fresh leaf disk. Only 10 of the 14 species had trichomes; *Acer* spp. and *Celastrus* spp. did not. SLA is a measure of leaf thickness. To measure SLA (mm2 mg-1), the leaf discs from the trichome count were dried at 45°C overnight and

weighed to determine dry mass. Higher SLA values indicate thinner leaves and thinner leaves are expected in shaded conditions to maximize leaf area for light capture.

Analyses

We present two separate analyses. The first analysis examines plasticity indirectly to ask whether origin explains patterns of plasticity. The second analysis directly quantifies plasticity.

Analysis I: Does origin explain patterns of plasticity?

To account for both correlations among traits and the inflated risk of type I error due to multiple tests, we initially analyzed all of the trait data with a multivariate analysis of variance (MANOVA). The main effects in the model included competition (low or high), nutrients (no addition or addition), origin (native or non-native) and genus (7 genera). The MANOVA was followed by univariate ANOVAs in which we considered all effects as fixed. All analyses were conducted with JMP (Version 7, SAS Institute Inc., Cary, NC, 2007).

Note that this analysis does not directly quantify the magnitude of the plastic response, but rather focuses on interaction terms for evidence of plasticity. A significant main effect of origin (or genus) indicates that natives and weedy non-natives (or genera) differ in their trait means, while an origin x genus interaction indicates that species differ in their trait means. A significant main effect of competition or nutrients indicates that plasticity has occurred (i.e., the environmental manipulation impacted trait values). A significant origin x competition or origin x nutrients interaction indicates that natives and weedy non-natives differentially responded to the environmental manipulations, and would thus suggest that weediness

is a good predictor of plasticity. A significant genus x competition or genus x nutrients interaction suggests that genera vary in their plastic responses.

We excluded the four-way interaction and two of the three-way interactions because they were not significant in the MANOVA or the ANOVAs. We did not, however, exclude the genus x origin x environment interactions, because they were important to our interpretation of the results. If either of these three way interactions was significant that would indicate that species differed in their plasticity, and thus that plasticity was not conserved within genera.

Finally, because there were 12 tests each of the hypotheses that origin or genus best explained plasticity (*i.e.,* 6 traits x 2 origin by environment terms, or 6 traits x 2 genus by environment terms), we addressed the inflated risk of type I error with a binomial expansion test (Sokal & Rohlf, 1994).

For Analysis I, we ln +1 transformed all data to improve the normality of the residuals and then standardized trait values by converting them to z-scores, using:

$$(x_i - \mu_x) / \sigma$$

where x_i is the data point, μ_x is the mean trait value for a given species, and σ is the standard deviation of that trait and species. We standardized the data to address two issues. First, we were concerned that the large variation in trait means across all 14 species would drive the patterns of plasticity we saw and obscure origin x environment interactions. Second, some of the traits (total length and RGRmax) were measured differently on different species, because of variation in morphology (i.e., rosettes versus branching plants). Standardizing the traits within species would facilitate comparisons across species. Running the model with data that were not standardized did not change our final interpretation of our results.

Analysis II: Direct estimation of the plastic responses

Our indirect measure of plasticity depends on the genus x environment interaction term. If only one genus responded to the environmental manipulations, we would still detect a significant genus x environment interaction. Thus, to directly assess differences in plasticity, we also quantified the amount and direction of plasticity for each species using within study factorial meta-analysis techniques (Gurevitch et al., 2000; Van Zandt, 2007). While there are many metrics for quantifying plasticity (Valladares et al., 2006), the metric employed in a factorial meta-analysis, Hedges' d, offers several advantages. First, Hedges' d corrects for sample size and sampling variance, so we were able to take into account the differences in replication amongst the species employed in this experiment. Second, Hedges's *d* measures the strength and direction of a trait response in units of standard deviation, making it easier to compare the plasticity of different traits on the same scale. One can also calculate 95% confidence intervals around a Hedge's d value to enable comparisons across traits and species.

RESULTS

The MANOVA (Table 1.2) indicated that plants responded to the environmental manipulations, and that competition and nutrients independently impacted plant traits. Natives and non-natives did not generally differ in plasticity (i.e., non-significant origin x competition and origin x nutrients terms). In contrast, relatedness was a good predictor of variation in plasticity (i.e., significant genus x competition and genus x nutrients interaction terms) and species within a genus had similar plasticity (non-significant genus x origin x environment interaction terms).

Table 1.2 Multivariate analysis of variance on all six plant traits. F-values were approximated from Wilks' λ. Significant model factors are highlighted in bold.

	Effect	DF	F	P
	whole model	**180**	**3.1**	**<0.0001**
Did native or non-natives, or genera or species differ in trait means?	origin	6	0.9	0.499
	genus	**24**	**4.3**	**<0.0001**
	genus x origin	24	1.5	0.054
Did the traits respond to competition or nutrients?	**competition**	**6**	**9.6**	**<0.0001**
	nutrients	**6**	**9.8**	**<0.0001**
	competition x nutrients	6	1.9	0.073
Did native and non-natives differ in plasticity?	origin x competition	6	0.7	0.648
	origin x nutrients	6	0.7	0.631
Did genera differ in plasticity?	**genus x competition**	**24**	**5.8**	**<0.0001**
	genus x nutrients	**24**	**3.2**	**<0.0001**
Did species within genus differ in plasticity?	genus x origin x competition	24	0.6	0.934
	genus x origin x nutrients	24	1.1	0.344

Univariate ANOVAs (Table 1.3) showed that plant traits responded plastically to the environmental manipulations. In response to reduced competition, the plants gained 73% more leaf mass (2.6 g ± 0.2 s.e.m. versus 1.5 ± 0.1 with competition), grew 28% larger (total length: 72.5 ± 8.3 versus 56.7 cm ± 5.8 s.e.m.) and produced 9% denser leaves (SLA: 19.7 mm2/mg ± 0.4 s.e.m versus 21.6 ± 0.5). In response to fertilizer addition, plants grew 9% more rapidly (RGRmax: 0.038 cm cm-1 day -1 ± 0.003 s.e.m. versus 0.035 ± 0.004 without fertilizer) and produced 8% thinner leaves (SLA: 21.4 mm2/mg ± 0.5 s.e.m. versus 19.9 ± 0.4). They also produced more 115% more leaf mass (2.8 g ± 0.2 s.e.m. versus 1.3 ± 0.1) and grew 93% longer (total length: 85.5 cm ± 9.2 s.e.m. versus 44.3 cm ± 4.3).

As in the MANOVA, the univariate ANOVAs found that origin predicted very little of the plasticity. Natives and non-natives only differed significantly in the plasticity of specific leaf area to fertilizer addition and this single significant effect may have occurred due to chance (Binomial expansion test, $P = 0.341$). Genus, in contrast, was a good predictor of the plasticity of total length, RGRmax, SLA, and trichomes in response to competition, and of plasticity of leaf mass (Figure 1.2), total length, and RGRmax in response to nutrients (Table 1.3). Seven significant genus x environment effects are highly unlikely to have occurred by chance (Binomial expansion test, $P < 0.0001$). Also, species within genera never varied in their trait plasticities suggesting that plasticity may be evolutionarily conserved (Table 1.3).

When we directly quantified plasticity using Hedge's d, we again found highly variable plasticity across genera (Table 1.4, Figure 1.3): the difference between the most to negative and most positive plasticity for a given trait and environment ranged from 1.1 3.1 units of standard deviation (Table 1.4).

Table 1.3 ANOVAs for plant traits, with significant factors highlighted in bold. Due to the data transformation none of the genus, genus x origin ("species"), or origin terms were significant (F-values ranged from 0.00 to 0.17) and were excluded from the table.

	Effect	Trait	df	F	p
Did traits respond to competition or nutrients?	competition	leaf mass	1	50.9	**<0.0001**
		length	1	4.9	**0.028**
		relative growth rate	1	1.4	0.236
		specific leaf area	1	13.0	**0.0003**
		toughness	1	1.1	0.289
		trichomes	1	0.5	0.471
	nutrients	leaf mass	1	40.0	**<0.0001**
		length	1	51.4	**<0.0001**
		relative growth rate	1	16.1	**<0.0001**
		specific leaf area	1	5.7	**0.018**
		toughness	1	2.4	0.123
		trichomes	1	3.0	0.084
	competition x nutrients	leaf mass	1	0.0	0.983
		length	1	1.0	0.327
		relative growth rate	1	2.2	0.138
		specific leaf area	1	3.3	0.069
		toughness	1	2.9	0.091
		trichomes	1	0.0	0.993
Did trait means differ among native and non-natives, among genera or among species?	origin	leaf mass	1	2.7	0.102
		length	1	0.4	0.531
		relative growth rate	1	0.9	0.353
		specific leaf area	1	0.0	0.926
		toughness	1	0.0	0.879
		trichomes	1	0.1	0.761
	genus	leaf mass	1	3.1	**0.005**
		length	1	3.4	**0.002**
		relative growth rate	1	5.3	**<0.0001**
		specific leaf area	1	0.1	0.990
		toughness	1	0.3	0.922
		trichomes	1	7.1	**<0.0001**
	genus x origin	leaf mass	1	0.7	0.622
		length	1	0.3	0.913
		relative growth rate	1	2.4	**0.028**
		specific leaf area	1	0.1	0.999
		toughness	1	0.1	0.998
		trichomes	1	0.2	0.957
Did native and non-natives differ in plasticity?	origin x competition	leaf mass	1	1.2	0.267
		length	1	0.1	0.783
		relative growth rate	1	2.3	0.128
		specific leaf area	1	0.4	0.530
		toughness	1	0.0	0.885
		trichomes	1	1.7	0.196

Table 1.3 continued

Did native and non-natives differ in plasticity	origin x nutrients	leaf mass	1	0.0	0.835
		length	1	0.0	0.965
		relative growth rate	1	0.2	0.654
		specific leaf area	1	6.1	**0.014**
		toughness	1	0.3	0.575
		trichomes	1	0.5	0.502
Did genera differ in plasticity?	genus x competition	leaf mass	1	1.4	0.232
		length	1	19.1	**<0.0001**
		relative growth rate	1	2.3	**0.033**
		specific leaf area	1	3.6	**0.002**
		toughness	1	1.8	0.089
		trichomes	1	2.9	**0.021**
	genus x nutrients	leaf mass	1	6.5	**<0.0001**
		length	1	5.6	**<0.0001**
		relative growth rate	1	3.4	**0.003**
		specific leaf area	1	1.9	0.075
		toughness	1	1.2	0.311
		trichomes	1	2.4	0.051
Did species within genera differ in plasticity?	genus x origin x competition	leaf mass	6	1.1	0.372
		length	6	1.1	0.337
		relative growth rate	6	1.0	0.401
		specific leaf area	6	1.9	0.077
		toughness	6	0.6	0.710
		trichomes	6	0.4	0.818
	genus x origin x nutrients	leaf mass	6	0.8	0.580
		length	6	1.5	0.164
		relative growth rate	6	0.8	0.600
		specific leaf area	6	1.6	0.156
		toughness	6	0.6	0.725
		trichomes	4	3.7	**0.006**

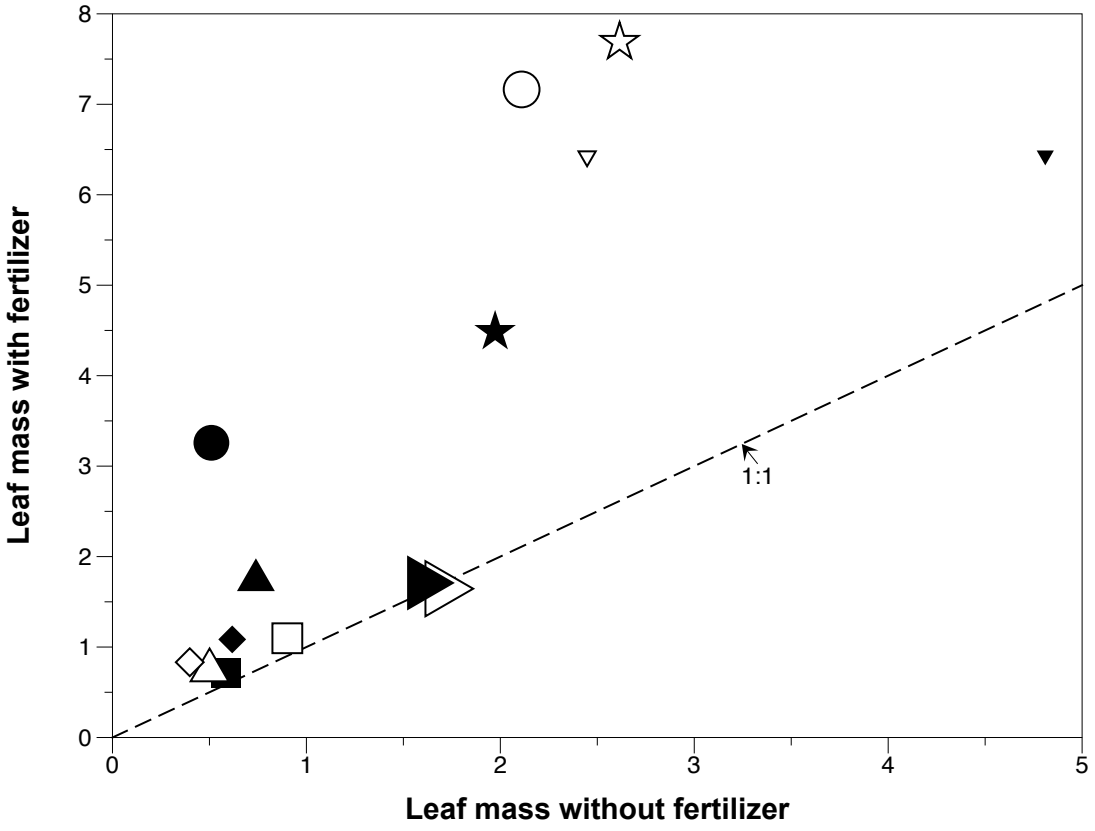

Figure 1.2 Mean leaf mass in plots with fertilizer versus plots without fertilizer. Each point represents a species with open symbols for non-natives and closed symbols for natives. Congeneric pairs share symbols (Acer – squares, Bromus – circles, Celastrus – up arrows, Elymus – diamonds, Plantago – large right arrows, Rosa – small down arrows, Solanum – stars). The dashed line indicates a 1:1 line. If a point falls along this line, then that species had no plasticity of leaf mass to the fertilizer (i.e., equal leaf mass in fertilizer and no fertilizer treatments). Species within genus had similar plasticity (Table 2 ANOVA: genus x nutrients $F = 6.5$, $P < 0.0001$). Within four genera (Acer, Celastrus, Elymus, and Plantago) the native and non-native pair cluster closely and show limited plasticity to fertilizer. For the remaining three genera, plasticity is larger and more variable within genus.

Table 1.4 Direct measures of trait plasticity using Hedge's *d* in units of standard deviation. Numbers in parentheses respresent the lower and upper bound of 95% confidence intervals. Significant Hedge's *d* values are highlighted in gray.

Trait	Genus	Species	Plasticity to C	Plasticity to N
leaf mass	*Acer*	*platanoides*	1.113 (0.634, 1.592)	0.381 (-0.09, 0.852)
		saccharum	1.231 (0.735, 1.727)	0.514 (0.027, 1.001)
	Bromus	*inermis*	0.806 (-0.107, 1.718)	1.403 (0.472, 2.333)
		latiglumis	0.255 (-0.658, 1.168)	0.688 (-0.231, 1.607)
	Celastrus	*orbiculatus*	0.757 (-0.021, 1.535)	0.45 (-0.324, 1.223)
		scandens	1.397 (0.759, 2.036)	1.007 (0.377, 1.637)
	Elymus	*repens*	0.142 (-0.45, 0.735)	0.71 (0.113, 1.307)
		trachycaulus	0.428 (-0.124, 0.979)	0.35 (-0.201, 0.901)
	Plantago	*major*	0.678 (-0.049, 1.406)	-0.068 (-0.791, 0.655)
		rugelli	0.359 (-0.167, 0.884)	0.052 (-0.473, 0.576)
	Rosa	*multiflora*	1.26 (0.326, 2.194)	1.355 (0.418, 2.292)
		palustris	1.637 (0.425, 2.848)	0.631 (-0.542, 1.804)
	Solanum	*dulcamara*	0.187 (-0.321, 0.695)	1.237 (0.717, 1.757)
		carolinense	0.806 (0.29, 1.321)	0.906 (0.389, 1.423)
RGR	*Acer*	*platanoides*	0.257 (-0.202, 0.717)	0.074 (-0.385, 0.533)
		saccharum	-0.118 (-0.584, 0.347)	0.181 (-0.284, 0.647)
	Bromus	*inermis*	-0.032 (-0.936, 0.871)	0.973 (0.056, 1.889)
		latiglumis	0.173 (-0.695, 1.041)	0.721 (-0.154, 1.595)
	Celastrus	*orbiculatus*	-0.244 (-0.951, 0.464)	0.41 (-0.299, 1.119)
		scandens	0.61 (-0.013, 1.234)	0.891 (0.263, 1.518)
	Elymus	*repens*	-0.776 (-1.338, -0.214)	0.032 (-0.525, 0.588)
		trachycaulus	0.018 (-0.507, 0.542)	-0.099 (-0.623, 0.426)
	Plantago	*major*	0.337 (-0.381, 1.055)	-0.087 (-0.804, 0.63)
		rugelli	0.684 (0.165, 1.203)	-0.246 (-0.762, 0.27)
	Rosa	*multiflora*	0.063 (-0.85, 0.975)	0.112 (-0.8, 1.025)
		palustris	1.035 (-0.079, 2.149)	0.482 (-0.618, 1.581)
	Solanum	*dulcamara*	0.332 (-0.167, 0.831)	-0.078 (-0.577, 0.42)
		carolinense	0.174 (-0.332, 0.681)	0.229 (-0.277, 0.736)
length	*Acer*	*platanoides*	0.876 (0.405, 1.347)	0.249 (-0.217, 0.715)
		saccharum	0.785 (0.295, 1.274)	0.491 (0.004, 0.978)
	Bromus	*inermis*	-0.904 (-1.888, 0.08)	0.168 (-0.804, 1.141)
		latiglumis	-1.27 (-2.177, -0.363)	0.916 (0.019, 1.813)
	Celastrus	*orbiculatus*	0.718 (-0.06, 1.495)	0.706 (-0.071, 1.483)
		scandens	1.247 (0.612, 1.881)	1.01 (0.381, 1.64)
	Elymus	*repens*	-1.19 (-1.795, -0.585)	0.638 (0.042, 1.234)
		trachycaulus	-0.924 (-1.481, -0.367)	0.148 (-0.402, 0.698)
	Plantago	*major*	-0.422 (-1.141, 0.297)	0.663 (-0.058, 1.384)
		rugelli	-0.404 (-0.934, 0.127)	0.208 (-0.322, 0.738)
	Rosa	*multiflora*	1.86 (0.901, 2.819)	1.28 (0.345, 2.215)
		palustris	1.406 (0.206, 2.606)	0.608 (-0.565, 1.781)
	Solanum	*dulcamara*	-0.226 (-0.729, 0.277)	1.264 (0.749, 1.779)
		carolinense	0.374 (-0.19, 0.938)	0.893 (0.324, 1.462)

Table 1.4 continued

Trait	Genus	Species	Plasticity to C	Plasticity to N
SLA	*Acer*	*platanoides*	0.283 (-0.187, 0.753)	0.308 (-0.162, 0.778)
		saccharum	-0.628 (-1.116, -0.14)	0.369 (-0.117, 0.855)
	Bromus	*inermis*	-0.234 (-1.164, 0.697)	-0.447 (-1.38, 0.485)
		latiglumis	0.062 (-0.823, 0.948)	0.38 (-0.508, 1.267)
	Celastrus	*orbiculatus*	-1 (-1.783, -0.217)	0.873 (0.093, 1.653)
		scandens	-0.119 (-0.739, 0.501)	0.595 (-0.028, 1.218)
	Elymus	*repens*	-0.468 (-1.062, 0.126)	0.592 (-0.004, 1.187)
		trachycaulus	-0.619 (-1.167, -0.071)	0.807 (0.257, 1.357)
	Plantago	*major*	-1.189 (-1.919, -0.459)	-0.556 (-1.276, 0.164)
		rugelli	-1.443 (-1.996, -0.891)	0.537 (-0.001, 1.074)
	Rosa	*multiflora*	0.215 (-0.698, 1.128)	0.085 (-0.827, 0.998)
		palustris	0.348 (-0.821, 1.516)	0.198 (-0.969, 1.365)
	Solanum	*dulcamara*	0.125 (-0.383, 0.632)	0.123 (-0.384, 0.63)
		carolinense	-0.604 (-1.158, -0.05)	0.101 (-0.45, 0.652)
toughness	*Acer*	*platanoides*	-0.198 (-0.664, 0.268)	-0.129 (-0.595, 0.337)
		saccharum	0.229 (-0.257, 0.714)	0.19 (-0.295, 0.676)
	Bromus	*inermis*	0.346 (-0.627, 1.32)	0.305 (-0.668, 1.278)
		latiglumis	-0.009 (-0.895, 0.877)	0.493 (-0.395, 1.382)
	Celastrus	*orbiculatus*	-0.364 (-1.121, 0.394)	-0.174 (-0.93, 0.583)
		scandens	0.158 (-0.462, 0.778)	-0.487 (-1.109, 0.135)
	Elymus	*repens*	0.366 (-0.333, 1.065)	-0.224 (-0.922, 0.475)
		trachycaulus	0.494 (-0.107, 1.095)	0.046 (-0.552, 0.645)
	Plantago	*major*	0.572 (-0.148, 1.292)	-0.222 (-0.94, 0.495)
		rugelli	0.459 (-0.073, 0.991)	-0.598 (-1.131, -0.064)
	Rosa	*multiflora*	0.215 (-0.698, 1.127)	-0.005 (-0.918, 0.907)
		palustris	-0.284 (-1.381, 0.813)	-0.532 (-1.632, 0.569)
	Solanum	*dulcamara*	-0.251 (-0.754, 0.252)	-0.627 (-1.133, -0.121)
		carolinense	-0.3 (-0.831, 0.231)	-0.233 (-0.764, 0.297)
trichomes	*Acer*	*platanoides*	n/a	n/a
		saccharum	n/a	n/a
	Bromus	*inermis*	-0.611 (-1.546, 0.324)	-0.535 (-1.469, 0.398)
		latiglumis	0.285 (-0.602, 1.172)	0.084 (-0.802, 0.97)
	Celastrus	*orbiculatus*	n/a	n/a
		scandens	n/a	n/a
	Elymus	*repens*	-0.656 (-1.245, -0.068)	0.015 (-0.569, 0.6)
		trachycaulus	-0.157 (-0.702, 0.388)	-0.021 (-0.565, 0.524)
	Plantago	*major*	-0.031 (-0.748, 0.686)	1.019 (0.292, 1.745)
		rugelli	0.056 (-0.468, 0.581)	0.354 (-0.172, 0.879)
	Rosa	*multiflora*	0.541 (-0.375, 1.458)	1.171 (0.24, 2.102)
		palustris	0.534 (-0.637, 1.706)	0.402 (-0.768, 1.571)
	Solanum	*dulcamara*	0.346 (-0.158, 0.849)	0.59 (0.085, 1.095)
		carolinense	0.689 (0.134, 1.244)	-0.483 (-1.035, 0.07)

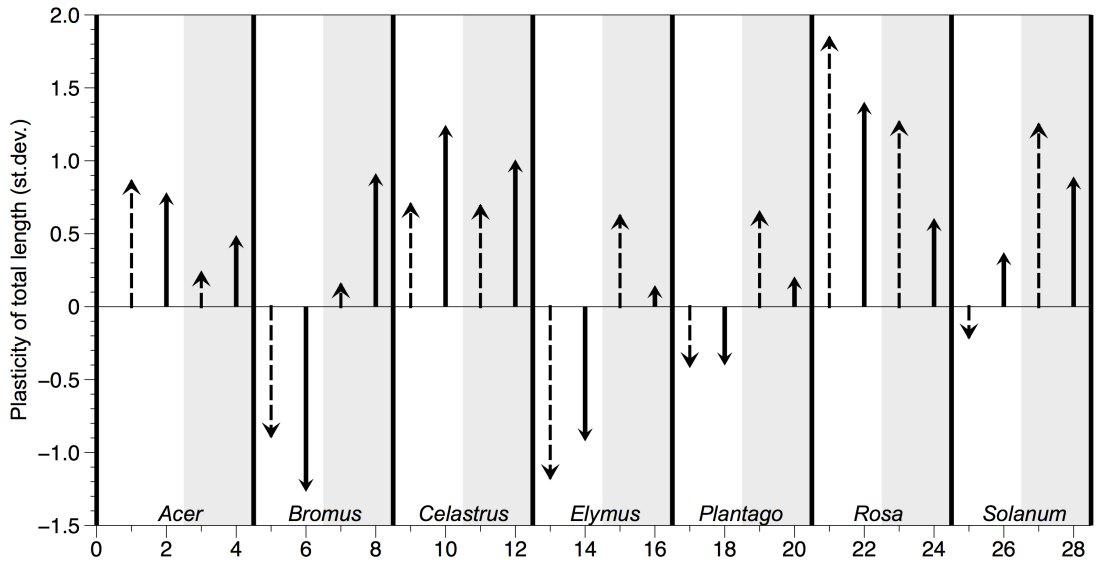

Figure 1.3 The plasticity of total plant length to competition and nutrients. To illustrate the conservation of plasticity with genus, we show here the Hedge's d, which directly quantify the plasticity of total length to competition and fertilizer. The length of the arrow indicates the magnitude of trait change in response to the environmental treatments. Light columns indicate plasticity to competition and dark columns indicate plasticity to fertilizer. Columns are organized by genus, with the non-native species first (dashed arrows) and the native species second (solid arrows). The full dataset (with 95% confidence intervals) for each of the traits is given in Table 1.4.

DISCUSSION

This experiment employed seven pairs of native and weedy non-native plant congeners to test whether origin predicted variation in plasticity among species. We found very little evidence that weedy non-natives were more plastic than related natives for the traits and environments tested. Instead, we found more evidence that genera differ in their plasticity, suggesting that plasticity may be conserved among related species.

Several recent analyses of plasticity in invasive species have found results consistent with our results. Palacio-López and Gianoli (2011) conducted a meta-analysis of plasticity in 93 species pairs (of which 43% were congeneric pairs) and found that invasives were not more plastic than natives or non-invasive non-natives to light, nutrients, water, CO_2, herbivory, or the presence of a climbing support upon which to grow. Godoy et al (2011) examined plasticity to light and nutrients in 20 invasive-native pairs (of which 25% were congeners), and also found that invasives were not generally more plastic than natives. In contrast, Davidson et al (2011) conducted a meta-analysis with 75 pairs of species, a quarter of which were congeners. They found that the invasives had higher plasticity than natives or non-invasive non-natives to nutrients, light, water, competition, disturbance, CO_2, presence of a climbing support, and presence of soil biota. Differences among these studies may be a function of the traits analyzed, as plastic responses are specific to the traits measured and the environments in which they are measured (Bradshaw, 1965; Schlichting, 1986). However, it is clear that weedy or invasive species are not consistently more plastic than non-weedy natives or non-natives.

While native and weedy non-native species did not differ in their plasticity in this experiment, genera did. This suggests that related species share similar patterns of

plasticity. Nonetheless, there are studies that examine a single genus and find differential plasticity among closely related species. For example, Valladares et al. (Valladares et al., 2000) showed highly variable plasticity among 16 tropical shrubs from the genus *Psychotria* and attributed differences in plasticity to their affinity for gap or understory habitats. Other single-genus studies have found differential plasticity among congeners and have attributed those differences to the invasive status of the species (e.g. Brock et al., 2005; Davidson et al., 2011; Geng et al., 2006; Leicht-Young et al., 2007; Schweitzer & Larson, 1999). These examples of differential plasticity among closely related species suggest that phenotypic plasticity evolves rapidly, in which case we would not expect to see a phylogenetic signal for plasticity. However, if plasticity evolves within a genus only to a limited extent and is ultimately constrained by evolutionary history, then we would detect a phylogenetic signal when comparing species at a broader phylogenetic scale (*e.g.*, across genera). Indeed, Kembel and Cahill (2005) measured root plasticity in 102 species from multiple families and found a strong signal of phylogenetic conservatism for root proliferation in response to nutrients. Ultimately, a more extensive phylogenetic study would help elucidate patterns of plasticity evolution and show at what level of relatedness we might expect to see conservation *versus* lability of plasticity.

All of the species we studied grow in relatively open fields and may share patterns of plasticity due to similar habitat affinities rather than shared evolutionary history. Plasticity in plants has long been attributed to the type of habitat in which that plant grows (Grime, 1977). For example, Van Zandt (2007) compared nine pairs of congeners where each pair contained a species from a resource-limited glade habitat and a species from a more productive, non-glade habitat. He found that species from non-glade habitats generally had higher plasticity in chemical defenses than those from glade habitats. Thus, in this example, habitat was a better predictor of plasticity

than phylogenetic relatedness. However, others have compared species from very different habitats and found that evolutionary history still explained a significant portion of the variation in plasticity (Hoffmann & Franco, 2003). Because the 14 species in our experiment are from very similar habitats, we removed variation due to habitat affinity, thus providing additional control in our test of the impacts of evolutionary history and weediness on plasticity.

In conclusion, genus was a better predictor of plasticity than origin for the combination of traits, species, and environments that we tested. These results suggest that it may be better to examine evolutionary relationships rather than continental origin when trying to predict species traits. If plasticity does indeed contribute to spread of non-native species, then a potential invader that is closely related to highly plastic natives may be of more concern than one that is related to less plastic natives.

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CHAPTER 2

EXOTIC PLANTS CONTRIBUTE POSITIVELY TO BIODIVERSITY FUNCTIONS BUT MAY HARM THE LONG-TERM SUCCESS OF NATIVE COMMUNITIES

Susan C. Cook-Patton and Anurag A. Agrawal

ABSTRACT

Although exotic plants comprise a substantial portion of floristic biodiversity, their contributions to ecosystem and community processes are not well understood. We manipulated plant species richness in old-field communities to compare the impact of exotic versus native diversity on primary production, fruit production, and arthropod community structure. Regardless of whether the species were native or exotic, increasing plant diversity enhanced productivity, fruit production and arthropod diversity. In addition, positive and complementarity interactions among species drove the gains in productivity and fruit production in both native and exotic polycultures. However, when exotic and native species were grown together, we found that exotics suppressed fruit production in natives. In addition, exotics attracted fewer arthropod species for a given arthropod abundance than did natives. Thus, exotics appear to contribute positively to some functions, but may harm the long-term success of native communities by reducing native fitness and recruiting fewer arthropod species.

INTRODUCTION

Plant diversity is rapidly changing in many communities as a result of the extirpation of native species and the introduction of exotics (Pimm et al. 1995; Sala et al. 2000). Although there are several cases in which exotic introductions reduced diversity in communities by displacing natives (Mack et al. 2000), there are also many

examples of exotic plant species becoming integrated into communities, thereby increasing rather than decreasing the overall species richness (Sax et al. 2002; Ellis et al. 2012). For example, in the last 200 years, plant diversity in the Cayuga Region of New York (USA) has increased over 50% due to the introduction of 777 exotic species, with few, if any, extinctions (Marks et al. 2008). Although many biodiversity experiments have included exotics in their species pools (*e.g.,* Tilman et al. 1996; Dukes 2001; Reich et al. 2001; Fridley 2002), the authors do not examine the specific contributions of exotics to the observed results. There has been remarkably little experimental attention to determine explicitly the effect of exotic biodiversity on ecosystem function and community structure (Wilsey et al. 2009; Wilsey et al. 2011).

Many years of theoretical and experimental work have shown a strong link between biodiversity and ecosystem functioning, and in particular, a positive and saturating relationship between plant biodiversity and productivity (Tilman et al. 1996; Hooper et al. 2005; Cardinale et al. 2011). Potential mechanism behind this positive diversity-productivity relationship (Loreau & Hector 2001; Fox 2005) include an increased probability of including a highly productive species with increasing plant diversity (*i.e.,* the *sampling effect*), increased dominance by one or a few species in mixtures (*i.e.,* the *selection effect*, which in Fox's (2005) terminology is partitioned into *trait-dependent complementarity* and the *dominance effect*), or reduced competition in mixtures due to niche partitioning, facilitation or other positive interactions among species (*i.e.,* "complementarity" or "trait-independent complementarity" *sensu* Fox 2005; Cardinale et al. 2011).

There are several reasons why we might expect diversity-productivity relationships and the mechanisms underlying them to vary between native-dominated and exotic-dominated assemblages. First, native plants have likely interacted with each other and their environment for millennia, whereas most exotic species arrived to the United States with European settlement of the New World (Mack & Lonsdale 2001). Additionally, the exotic plant species in the United States evolved in locations from across the globe, suggesting that they are less likely to have co-occurred historically. Finally, some exotics can be highly competitive or invasive (Levine et al. 2003) and thus may have negative impacts on co-occurring species, although there are many exotic species that integrate into the native matrix without suppressing natives (Davis et al. 2011).

Similar to ecosystem measures like primary productivity, community processes can also be modified by changes in plant diversity. In particular, increasing plant diversity has been shown to impact the diversity of dependent arthropod communities (Tahvanainen & Root 1972; Andow 1991; Haddad et al. 2001; Cook-Patton et al. 2011). Two potential mechanisms can explain this pattern. First, total resource availability may determine arthropod species richness (*more individuals hypothesis,* Srivastava & Lawton 1998). If diverse plant communities are more productive and thus recruit more individual arthropods, then arthropod richness may be higher due to an increased probability of observing rare arthropods. Second, if arthropods are attracted to specific plant species, then increasing plant diversity may recruit a more diverse fauna (*resource specialization hypothesis*, Hutchinson 1959; Murdoch et al. 1972; Strong et al. 1984). To our knowledge, there have been no direct experimental

comparisons of how changes in native and exotic plant diversity impact arthropod community structure. We predicted that resource-driven accumulation of species would apply in both native and exotic communities, but that resource specialization dynamics would occur more often in native-dominated rather than exotic-dominated plant communities because exotic plant species may have lost most of their specialist fauna while migrating to the new range (Keane & Crawley 2002).

To investigate whether changes in native and exotic diversity differentially impacted primary production, fruit production, and arthropod community structure we conducted a two-year field experiment. We established plant assemblages that were either monocultures (containing only one native or one exotic species), single-origin polycultures (containing either eight native or eight exotic species) or mixed-origin polycultures (containing four native and four exotic species). This study is an advance over previous work in that we (1) measured fruit production, in addition to plant biomass, to inform how these systems may respond to changes in diversity over longer time scales, (2) included a mixed-origin polyculture to address how the performance of natives is altered by the presence of exotics (and *vice versa*) and (3) analyzed arthropod richness and abundance to determine how changes in native and exotic plant biodiversity cascaded to higher trophic levels. Thus, this study is a thorough analysis of how exotic biodiversity, a significant but under evaluated fraction of plant biodiversity, impacts the short and long term functioning of native ecosystems.

METHODS

Study species and experimental design

We selected 32 species for this experiment (Table 2.1), which commonly co-occur in old-fields in central New York (Cook-Patton *pers. obs*). The majority of species employed were herbaceous forbs (with the exception of the two *Elymus* grasses) and there were no legumes. In retrospect, we know that the native and exotic species pools did not differ dramatically, because we measured twelve different functional traits in the monocultures during the field season (Table 2.2). We found that of the traits measured (time to bolt, time to flower, flowering duration, height, branch number, internode length, biomass, trichome density, leaf toughness, specific leaf area, leaf damage), only time to flower differed on average between natives and exotics ($p = 0.037$). Although this result suggests that exotics flowered earlier than natives, one significant trait out of eleven tested may have occurred by chance (binomial expansion test, $p = 0.329$).

We collected most seeds from populations around Ithaca, NY (USA) in 2007 and pooled seeds across multiple individuals and populations. The exceptions were *Elymus trachycaulus* and *E. repens* seeds, which derived from southern Ontario (Canada). In April 2008, we cold-stratified seeds (4°C, four days), sowed them into 96-well trays filled with soil (Pro-mix "BX" with biofungicide, Premier), and thinned seedlings to a single individual per well. In the greenhouse (14:10 hour light:dark cycle, 5 weeks), plants received water *ad libitum* and weekly fertilizer (21-5-20 NPK,

Table 2.1 Native and exotic species employed in the experiment.

Family	Species	Origin[a]	Replant (%)	ABP?[a]	Type[a]
Apiaceae	*Daucus carota*	E	87	B	forb
Apocynaceae	*Asclepias syriaca*	N	77	P	forb
Asteraceae	*Centaurea stoebe*	E	0	BP	Forb
	Cichorium intybus	E	0	BP	forb
	Eupatorium perfoliatum	N	0	P	forb
	Eupatoriadelphus maculatus	N	0	P	forb
	Leucanthemum vulgare[b]	E	100	P	forb
	Rudbeckia hirta	N	3	ABP	forb
	Solidago altissima	N	0	P	forb
	Solidago juncea	N	0	P	forb
	Symphyotrichum lanceolatum	N	0	P	forb
	Symphyotrichum novae-angliae	N	3	P	forb
Campanulaceae	*Campanula rapunculoides*	E	3	P	forb
	Lobelia inflata	N	100	P	forb
Caryophyllaceae	*Dianthus armeria*	E	3	AB	forb
	Saponaria officinalis	E	3	P	forb
	Silene vulgaris	E	3	P	forb
Clusiaceae	*Hypericum perforatum*	E	0	P	forb
	Hypericum punctatum	N	10	P	forb
Dipsaceae	*Dipsacus sativus & D. laciniatus*[c]	E	0	B	forb
Lamiaceae	*Clinopodium vulgare*	N	0	P	forb
	Prunella vulgaris	E*	8	P	forb
Onagraceae	*Epilobium coloratum*	N	5	P	forb
	Epilobium parviflorum	N	8	P	forb
Plantaginaceae	*Penstemon digitalis*	N	0	P	forb
	Oenothera perennis	N	3	P	forb
Poaceae	*Elymus repens*	E	38	P	grass
	Elymus trachycaulus	N	38	P	grass
Polygonaceae	*Rumex crispus*	E	8	B	forb
Scrophulariaceae	*Linaria vulgaris*	E	0	P	forb
	Verbascum blattaria	E	58	B	forb
	Verbascum thapsus[b]	E	n/a	B	forb
Verbenaceae	*Verbena hastata*	N	0	BP	forb

[a] Species information based on the USDA Plants Database (http://plants.usda.gov/); ABP refers to whether plants are annual (A), biennial (B), and perennial (P). Species that had completed their life cycle or had died in 2008 were replanted in 2009. The percent replanted is given in the fourth column.

[b] All of the *Verbascum thapsus* died in the first year and were replaced in 2009 with another exotic species that better tolerated conditions, *Leucanthemum vulgare.*

[c] The seed source for *Dipsacus sativus* was contaminated with *D. laciniatus*. Both species occurred in monoculture and in polyculture, so we used monoculture values specific to each species when calculating complementarity and dominance effects.

* Prunella vulgaris is a circumpolar species. The native form is Prunella vulgaris var. lanceolata. We used an exotic variety, Prunella vulgaris var. vulgaris.

Table 2.2 Mean trait values ± standard deviation for natives and exotics in monoculture. The p-values indicate whether trait means for natives and exotics significantly differed. All traits except relative fruit production, time to flower, flower duration, and height were ln + 1 transformed to improve the normality of the residuals before conducting the ANOVA.

Trait	**Exotic**	**Native**	**p-value**
time to bolt (days)	40.5 ± 32.5	26.7 ± 9.6	0.1290
time to flower (days)	84.8 ± 19.5	99.2 ± 30.6	**0.0370**
flower duration (days)	42.7 ± 26.0	37.3 ± 13.4	0.2408
height (cm)	79.8 ± 59.6	85.7 ± 43.6	0.2019
number of branches	6.3 ± 6.2	6.9 ± 4.7	0.2262
internode length (cm)	18.3 ± 20.1	14.8 ± 12.2	0.5461
biomass (g)	61.6 ± 96.5	49.9 ± 38.9	0.3027
trichomes (hairs cm^{-1})	12.1 ± 20.8	15.0 ± 14.5	0.1130
toughness	103.0 ± 28.5	123.0 ± 57.4	0.5613
damage (percent plant tissue consumed)	10.7 ± 7.1	17.8 ± 15.1	0.0565
SLA ($mm^2\ mg^{-1}$)	24.3 ± 8.0	25.2 ± 9.2	0.9883

150 ppm). One week prior to planting in the field, we field-hardened the plants in an outdoor mesh cage.

In June 2008, we established the experiment in an abandoned agricultural field near Dryden, NY (42º27'49" N, 76º26'19" W) where the soil was plowed, but otherwise untreated. All experimental plots contained eight individual plants in a 0.5m diameter ring and were separated from other plots by 1m. All species were represented in two monocultures initially, but due to mortality *Lobelia inflata*, and *Silene vulgaris* appeared only once in monoculture and *Asclepias syriaca* not at all (N = 60 monocultures remaining). In addition, *Dipsacus sativus* inadvertently contained a few *Dipsacus laciniatus* individuals (Table 2.1). Polycultures contained eight different species and consisted of two main types: single-origin polycultures (either all native species, N = 28, or all exotic species, N = 30) or mixed-origin polycultures with half native/half exotic species (N = 31). We generated polyculture assemblages randomly, but then adjusted the communities so that species occurred with fairly equal frequency across plots.

In June 2009, we replaced annuals and biennials that had completed their life cycle in the first year (*Lobelia inflata* and *Daucus carota*), as well as individuals that had died (Table 2.1). All *Verbascum thapsus* individuals died early in summer 2008, presumably because they could not tolerate the mesic soils; they were replaced in 2009 with *Leucanthemum vulgare.*

Plant performance

The first performance trait we measured was the number of fruits on each plant using a standardized protocol for each species. For example, for species with few,

conspicuous flowers we counted every individual fruit, but for species with large inflorescences, small flowers, and many seed heads (e.g., *Solidago altissima*) we counted every branch of the inflorescence.

The seccond performance trait we measured was aboveground plant biomass. We harvested the aboveground biomass of each individual plant between mid-September and mid-October 2009. We dried the tissue in a drying oven (65°C) for at least four days and weighed it to the nearest 0.1g. We also visually estimated damage thrice in 2009 (during each insect survey), using a 0-100% scale with 5% intervals, where 0% corresponded to no damage and 100% to consumption of all leaves and stems. We used the mean of the three damage estimates as a covariate in our model, because we expected tissue consumption to impact our aboveground productivity measures.

Insect surveys

Because arthropod communities change throughout the growing season, we surveyed arthropod communities thrice during 2009 (early June, mid-July and late-July). We carefully and fully scanned every plant to record the number and abundance of all arthropods visiting each plant. Arthropods were identified to species, if known, or to morphospecies, if unknown.

Statistical Analyses

All analyses were conducted with JMP (Version 7, SAS Institute Inc., Cary, NC, 2007), with the exception of the rarefaction analyses.

Hypothesis I: Diversity-productivity relationships will vary in native and exotic-dominated plots due to different underlying mechanisms.

To investigate overall primary production, we calculated total aboveground biomass in each plot and ln+1 transformed the data to improve the normality of the residuals. Because fruit production was quantified differently for each species, we first standardized the data to get relative fruit production (*i.e.*, x_i / μ_x, where x_i is the fruit production of an individual of species x and μ_x is the mean fruit production for species x). We then averaged relative fruit production within each plot. These data were analyzed with a two-way factorial ANOVA with origin (native or exotic) and diversity (monoculture or single-origin polyculture) as main effects. We included the damage estimate as a covariate since we expected tissue removal to impact aboveground tissue and fruit production. Note that this analysis excludes the mixed-origin polycultures, so that we could include the origin x diversity interaction. However, for completeness we note the mixed-origin polycultures' mean biomass and fruit production in the results.

Higher performance in diverse assemblages may be due to several mechanisms (Loreau & Hector 2001; Cardinale et al. 2011). *Positive complementarity* occurs when species in polyculture have, on average, higher performance than expected from monocultures. It has been attributed to niche partitioning or facilitation among species, but does not distinguish between these two mechanisms (Cardinale et al. 2011). In contrast, *positive selection* occurs when highly productive monoculture species disproportionately dominate in polyculture, whereas *negative selection* occurs when small monoculture species show the most gains. Fox (2005) further partitioned the selection effect into *trait-dependent complementarity* and *dominance effects*. *Trait-*

dependent complementarity occurs when one or a few species do disproportionately better in polycultures without suppressing the growth of other species, whereas the *dominance effect* occurs when the increased performance of one or a few species comes at the expense of the other species. Fox (2005) also changed the name of *complementarity* to *trait-independent complementarity* to distinguish it from *trait-dependent complementarity* and we employ his terminology throughout.

We modified these analyses slightly. First, we used the mean biomass (or fruit production, non-standardized) of a single plant in monoculture to calculate expected yields instead of the total biomass (or fruit production) of an entire monoculture (Cook-Patton et al. 2011). This modification allowed us to account for the contamination of the *Dipsacus sativus* seeds with *Dipsacus laciniatus*. Also, when a plant died and produced no biomass (or fruits) we replaced the zero values with a marginal non-zero value (0.001g) to facilitate calculations (Parker et al. 2010). Finally, we had no *Asclepias syriaca* monoculture data, so we set the expected yield of *A. syriaca* in polycultures equal to the observed yield. This means that *A. syriaca* did not contribute to the calculations of complementarity and dominance effects. Note that the fruit data used in this analysis were the raw (unstandardized) fruit counts because calculations of expected values already account for differences in species means. The tripartite partitioning method is outlined below with our modifications indicated in bold (Loreau & Hector 2001; Fox 2005; Long et al. 2007; Cook-Patton et al. 2011).

Define for any polyculture:

Mi	**average yield of an individual from species *i* in monoculture**
Y_{Oi}	observed yield of species *i* in the polyculture

$Y_O = \Sigma_i Y_{Oi}$	total observed yield of the polyculture
$RY_{Ei} = 1$	**relative yield of species *i* in polyculture is expected to be identical to that in monoculture**
$RY_{Oi} = Y_{Oi} / M_i$	observed relative yield of species *i* in the polyculture
$Y_{Ei} = RY_{Ei} \bullet Mi = M_i$	**expected yield of an individual from species *i* in the polyculture**
$Y_E = \Sigma_i Y_{Ei}$	total expected yield of the mixture
$RYT_O = \Sigma_i RY_{Oi}$	sum the observed relative yields of all species in the polyculture
$\Delta RY_i = RY_{Oi} - RY_{Ei}$	deviation from expected relative yield of species i in the polyculture
N	number of species in the polyculture

Trait-independent complementarity is calculated as $N \bullet \overline{\Delta RY_i \bullet M_i}$, trait-dependent complementarity is calculated as $N\mathrm{cov}\left(M_i, RY_{Oi} - {RY_{Oi}}/{RYT_O}\right)$, and the dominance effect is calculated as $N\mathrm{cov}(M_i, {RY_{Oi}}/{RYT_O} - RY_{Ei})$. The sum of these three terms is equal to the overall difference between the actual yield in polycultures and the expected yield calculated from monoculture value (*i.e.,* $Y_O - Y_E$).

Hypothesis II: Native plant performance will be impacted by the presence of exotics in mixed-origin polycultures (and vice versa)

For this analysis, we first calculated species means in the single-origin and mixed-origin polycultures. Each data point represented the mean biomass or relative fruit production of a species in the single-origin or mixed-origin polycultures. Thus,

replication is at the level of plant origin, allowing us to ask whether natives or exotics generally differed in performance in single-origin or mixed-origin polycultures. Because they produced biomass but no flowers or fruits, *Asclepias syriaca, Elymus repens,* and *Leucanthemum vulgare* were included in the analyses of biomass but not fruit production (N = 64 data points for biomass and 58 for fruit production). We also removed the three *Dipsacus laciniatus* individuals from the data, using the mean of the *Dipsacus sativus* data only. The biomass data were ln+1 transformed to improve the normality of the residuals, and all data were analyzed with a two-way factorial ANOVA with polyculture-type (single-origin or mixed-origin) and origin (native or exotic) as main effects.

Hypothesis III: Changes in native and exotic plant diversity will alter arthropod community structure via different mechanisms

We pooled the arthropod data across the three sampling times in 2009 and across all plants within each plot to generate cumulative richness and abundance data per plot. We used these data in factorial two-way ANOVAs with diversity (monoculture versus single-origin polyculture) and origin (native versus exotic) as main effects. Abundance was ln +1 transformed to improve the normality of the residuals. Note, that as with plant productivity, the mixed-origin polyculture data were excluded from these analyses.

To distinguish between the *more individuals* (Srivastava & Lawton 1998) and *resource specialization hypotheses* (Hutchinson 1959; Strong et al. 1984), we conducted further analyses. We examined the effect of plant biomass on arthropod

abundance by dividing arthropod abundance by the biomass of each plant and ln+1 transformed the resulting data to improve the normality of the residuals. We then analyzed these data with the same two-way ANOVA with origin and diversity as main effect. To determine whether the arthropod richness results were driven by differential abundances (Gotelli & Colwell 2001), we standardized the data to 10 individuals using individual-based rarefaction (*rarefy* in the R Vegan 1.17-3 package). We then analyzed the rarefied arthropod data with the same two-way ANOVA model and post-hoc contrasts.

RESULTS

Hypothesis I: Diversity-productivity relationships will vary in native and exotic-dominated plots due to different underlying mechanisms

Primary production in single-origin polyculture plots was 61% higher than in monoculture plots (Figure 2.1, diversity: $F_{1,114} = 41.9$, $p < 0.0001$) and there was no effect of plant origin (origin: $F_{1,114} = 1.6$, $p = 0.2141$). While, we predicted that the primary productivity of the natives would respond more positively to the diversity manipulation, we found the reverse trend: exotic polycultures produced 88% more biomass than exotic monocultures whereas native polycultures were only 35% more productive (diversity x origin: $F_{1,114} = 2.7$, $p = 0.1051$). Although not included in this statistical model, mixed-origin polycultures produced biomass intermediate to the single-origin polycultures with 64% more biomass than monocultures.

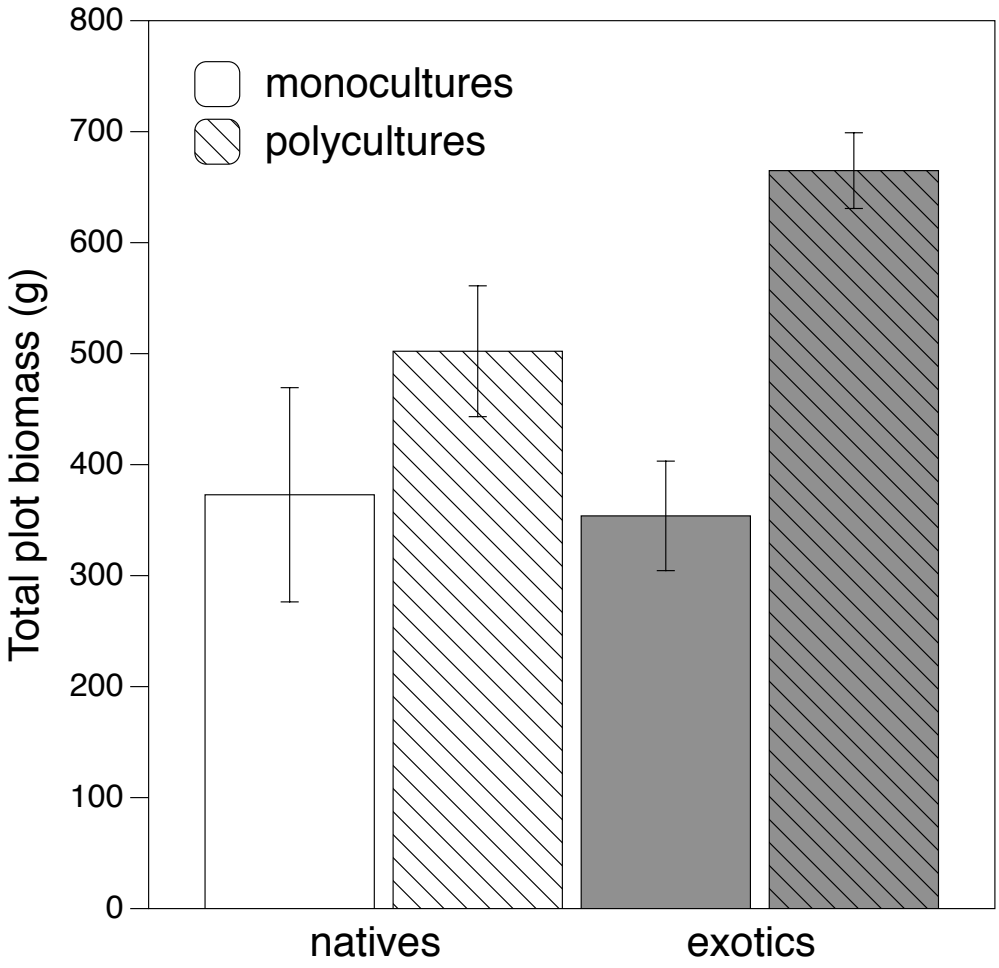

Figure 2.1 Mean total aboveground biomass for each diversity treatment in the single-origin monocultures and polycultures (means ± 1 s.e.m). White columns represent plots with native species and gray columns represent plots with exotics. Hatched lines indicate polycultures.

Relative fruit production was 54% higher in polycultures compared to monocultures (diversity: $F_{1,114} = 22.4$, $p < 0.0001$, diversity x origin: $F_{1,114} = 0.8$, $p = 0.3858$) and, in contrast to primary production, there was an effect of origin: across treatments, natives had 21% higher relative fruit production than exotics (origin: $F_{1,114} = 6.6$, $p = 0.0117$). Although not included in the statistical model, mixed-origin polycultures had 49% higher relative fruit production compared to monocultures.

When we examined the mechanisms underlying these performance results, we found that trait-independent complementarity was primarily responsible for the increases in biomass and fruit production (Figure 2.2) across all polyculture types (including mixed-origin polycultures; data given in Table 2.3). For biomass, we found trait-dependent complementarity and dominance effects to be small, with 95% confidence intervals that overlapped with zero. In contrast, for fruit production, there were significant negative trait-dependent complementarity and dominance effects in native-only (Fig. 2b) and mixed-origin polycultures (Table 2.3), indicating that species with low fruit production in monoculture disproportionately benefited in these two polyculture types. Exotic-only polycultures showed similar trends, but they were not significant (Table 2.3).

Hypothesis II: Native plant performance will be impacted by the presence of exotics in mixed-origin polycultures (and vice versa)

We found that natives produced equivalent biomass regardless of whether or not they grew with exotics (natives vs. exotics: $F_{1,62} < 0.1$, $p = 0.9960$). There was neither an effect of polyculture-type (single vs. mixed-origin polycultures: $F_{1,62} < 0.1$,

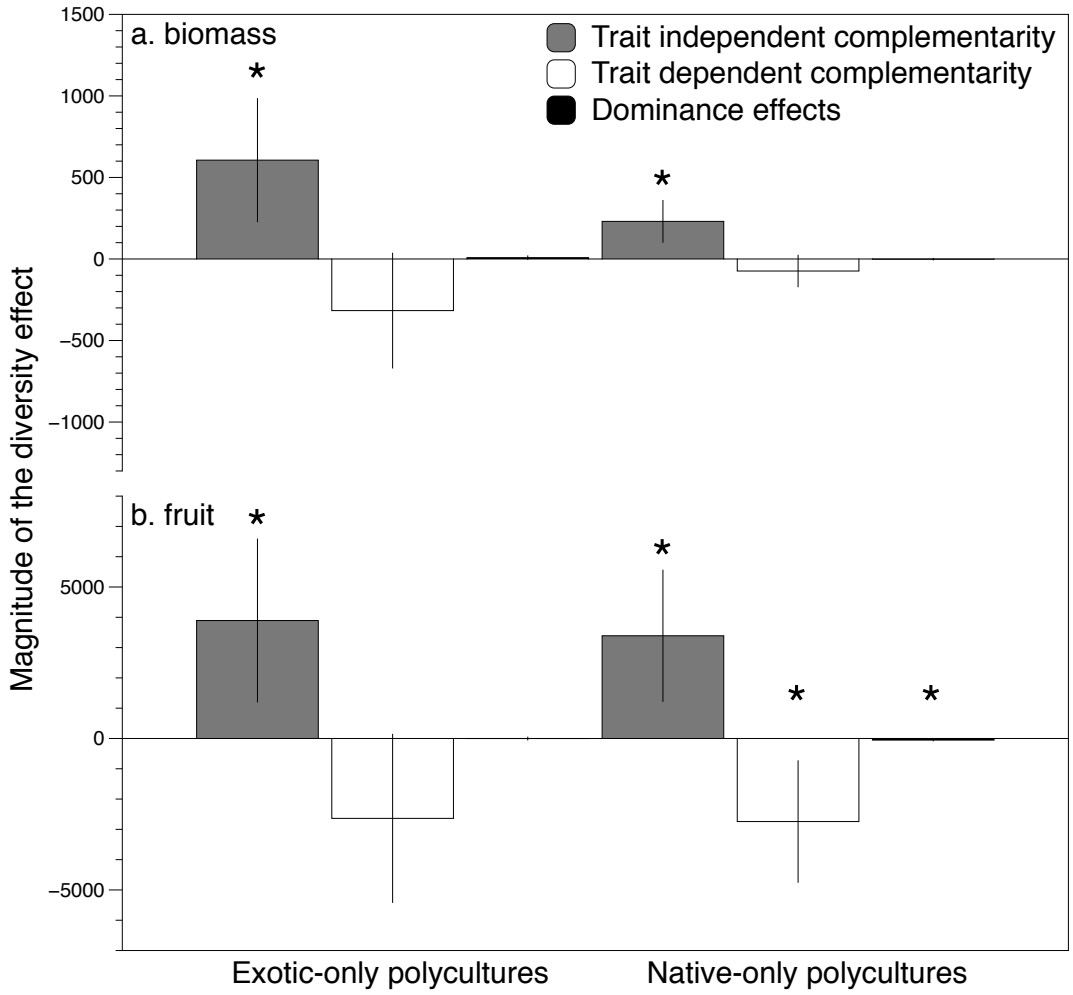

Figure 2.2 Mean trait-independent complementarity (TIC), trait-dependent complementarity (TDC) and dominance effects (DE) for total aboveground biomass (panel a) and fruit production (panel b) in the single-origin polycultures. From left to right mean TIC (gray), TDC (white), and DE (black). Error bars indicate 95% confidence intervals and stars indicate significant confidence intervals that do not overlap with zero. Raw means, including those for mixed-origin polycultures, are given in Table 2.3.

Table 2.3 Mean values of diversity mechanisms for biomass and fruit production in all polyculture types. Data represent means ± 95% confidence intervals and bolded numbers indicate confidence intervals that do not overlap with zero.

Biomass	**Complementarity**	**TDC**	**Dominance**
Native-only polyculture	**230.5 ± 127.9**	-73.8 ± 96.3	-1.2 ± 4.9
Exotic-only polyculture	**606.2 ± 377.4**	-316.6 ± 351.9	8.0 ± 10.8
Mixed-origin polyculture	**537.5 ± 331.6**	-287.9 ± 324.7	2.7 ± 8.2
Fruit			
Native-only polyculture	**3390.0 ± 2164.8**	**-2742.4 ± 2003.2**	**-52.5 ± 26.3**
Exotic-only polyculture	**3893.4 ± 2688.5**	-2637.4 ± 2774.6	-2.2 ± 46.5
Mixed-origin polyculture	**6927.9 ± 4907.2**	**-6048.4 ± 4789.3**	**-49.0 ± 27.2**

p = 0.7859), nor an interaction between the two main effects ($F_{1,62} < 0.1$, p = 0.9691). In contrast, exotics had 72% higher relative fruit production in mixed-origin polycultures than in exotic-only polycultures, but natives produced 20% less fruits in mixed-origin polycultures (origin x polyculture-type: $F_{1,54} = 5.7$, p = 0.0209, Figure 2.3). We observed no main effect of polyculture-type ($F_{1,54} = 0.3$, p = 0.6160) or origin ($F_{1,54} = 0.9$, p = 0.3497).

Hypothesis III: Changes in native and exotic plant diversity will alter arthropod community structure via different mechanisms

Similar to the plant biomass results, we found that arthropods were more abundant ($F_{1,115} = 29.7$, $p < 0.0001$; Figure 2.4a) and the communities more species-rich ($F_{1,115} = 68.4$, $p < 0.0001$; Figure 2.4c) in polycultures compared to monocultures. However, in general native plants did not accumulate more total arthropod individuals (abundance: $F_{1,115} = 0.4$, p = 0.5294) or species (richness: $F_{1,115} = 2.3$, p = 0.1245) than exotic plants; and there was no interaction between plant origin and diversity (abundance: $F_{1,115} = 0.5$, p =0.4860; richness: $F_{1,115} = 1.5$, p =0.2208).

To further explore how changes in native and exotic diversity affected arthropod community structure, we evaluated the influence of plant productivity on the number of arthropod individuals. After standardizing arthropod abundance by plant biomass, the previously significant effect of plant diversity on arthropod abundance disappeared (diversity: $F_{1,114} = 2.2$, p = 0.1387; origin: $F_{1,114} = 0.9$, p = 0.3345; diversity x origin: $F_{1,114} = 1.9$, p = 0.1676; Fig. 4b), indicating that higher

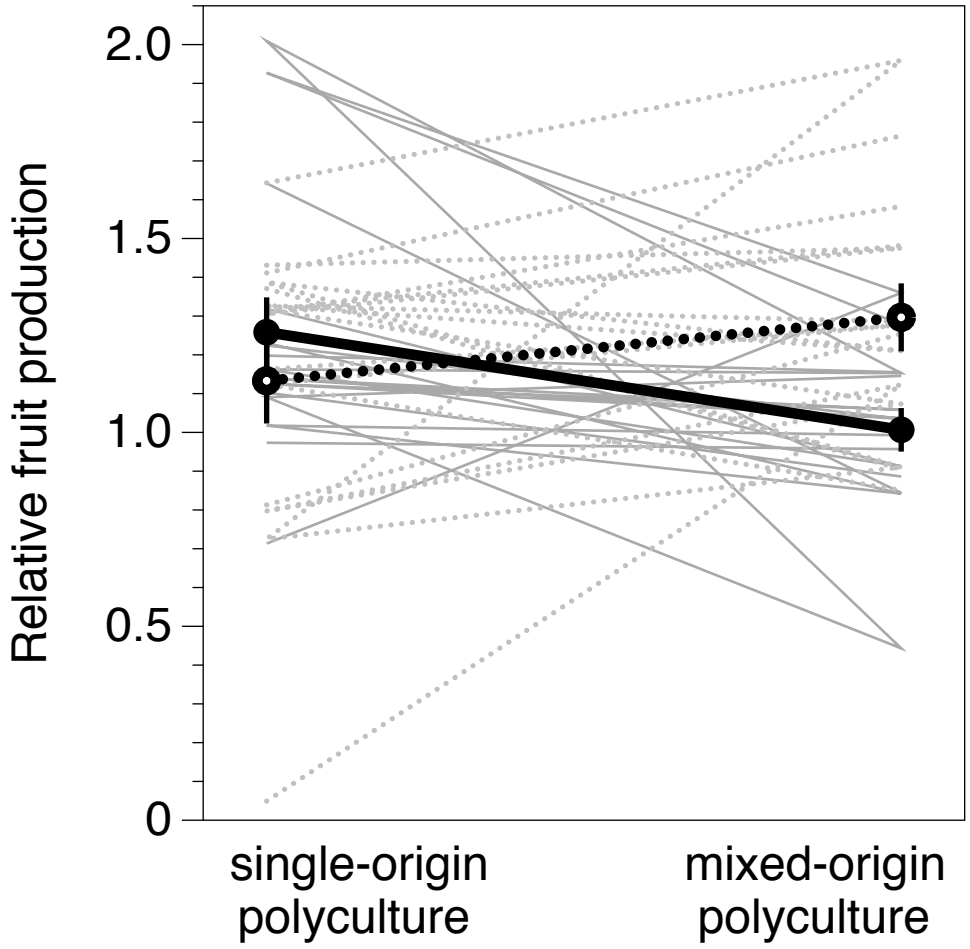

Figure 2.3 Reaction norms depicting the relative fruit production of native and exotic species in single-origin versus mixed-origin polycultures. Each dotted line indicates an exotic species and each solid line a native species. The dark lines with ± 1 s.e.m. error bars represent the mean relative fruit production of natives and exotic. Light gray lines indicate individual species responses.

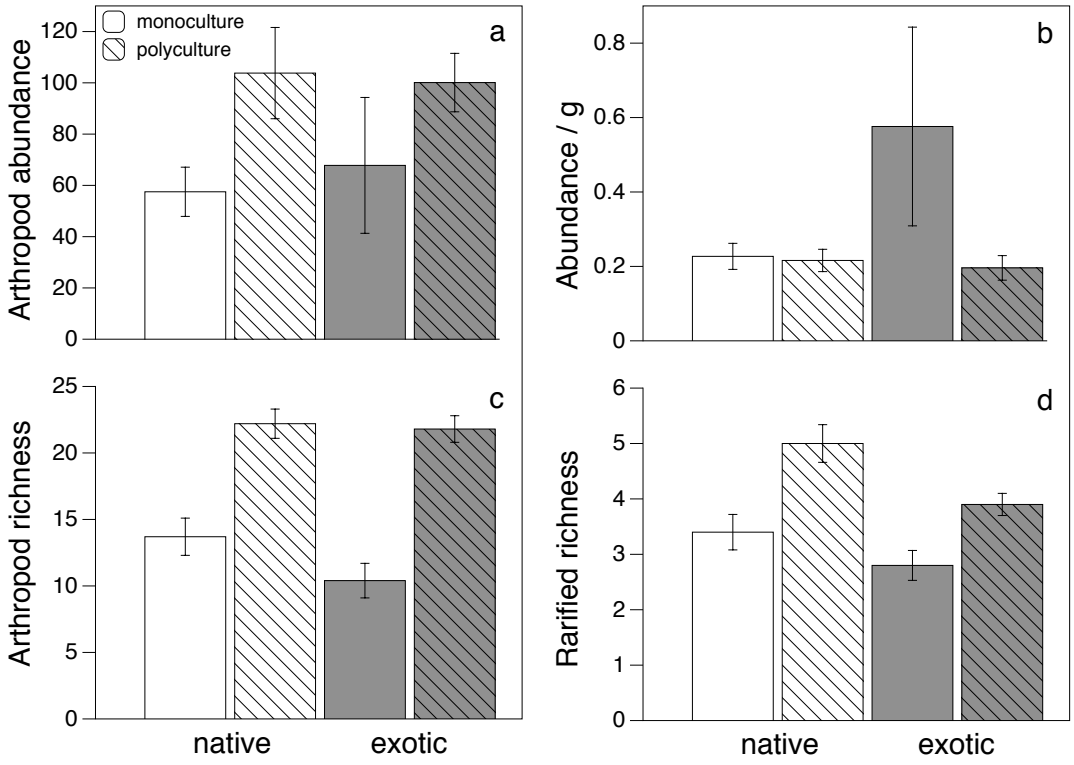

Figure 2.4 Response of arthropod community structure to changes in plant diversity and origin. White columns represent plots with native species and gray columns represent plots with exotics. Hatched lines indicate polycultures. (a) Arthropod abundance ± 1 s.e.m. (b) Mean arthropod abundance divided by plant biomass ± 1 s.e.m. There are no significant differences among these columns. (c) Mean arthropod richness in each treatment ± 1 s.e.m. (d) Rarified arthropod richness in each treatment ± 1 s.e.m.

arthropod abundance in diverse plots was driven primarily by increases in plant productivity rather than changes in plant diversity.

We next used rarefaction to determine whether increases in arthropod species richness were best explained by arthropod abundance (*more individuals hypothesis*) or by arthropod specialization on distinct host plants (*resource specialization hypothesis*). We found that rarefied species richness was still higher in polycultures by 45% compared to monocultures (diversity: $F_{1,115}$ = 23.1, p <0.0001; Fig. 4d), suggesting that diverse plant communities recruit a greater diversity of arthropods because they offer a greater diversity of resources (*resource specialization hypothesis*). In addition, this pattern was true for both native and exotic communities (diversity x origin: $F_{1,115}$ = 0.6, p =0.4103). Post-hoc contrasts showed that rarefied richness increased in both native ($F_{1, 115}$ = 15.4, p = 0.0001) and exotic ($F_{1, 115}$ = 8.1, p = 0.0052) polycultures compared to their respective monocultures. However, we found that rarefied richness was 24% higher in native plots than exotic plots ($F_{1,115}$ = 8.9, p =0.0035), suggesting that for a given abundance of arthropods, native plants recruit more different arthropod species than do exotic plants.

DISCUSSION

Exotic species are becoming an increasingly common component of our natural landscapes (Sax et al. 2002; Ellis et al. 2012) and our results suggest that they can have both positive and negative impacts on system functioning. Exotic polycultures were equally if not more productive than native polycultures and

recruited an equally abundant and diverse arthropod fauna as natives. However, exotic polycultures recruited fewer arthropod species when we controlled for differences in arthropod abundance through rarefaction. Furthermore, when exotics where grown with natives, they substantially reduced fruit production of co-occurring native species. We explore each of these results in detail below.

Counter to our predictions that the biomass of native communities would respond more strongly to the diversity manipulation than that of exotic communities, we found that biomass increased almost two-fold more in exotic polycultures than in native polycultures. Wilsey et al. (2009) found results consistent with this trend. They constructed monocultures and nine-species polycultures from a pool of 20 native and 20 exotic grassland species and also found that biomass increased more in exotic-only polycultures than native-only polycultures. However, the causal mechanisms differed between the two studies. We found that productivity gains in exotic polycultures were due to trait-independent complementarity (Fox 2005). In contrast, Wilsey et al. (2009) found that higher productivity in exotic polycultures resulted from a few large species becoming dominant and pushing out subordinates (*i.e*, selection effects). When Wilsey et al. (2011) conducted a similar follow-up experiment they found that exotic species competed more strongly than natives because they have more rapid and synchronous growth. We further examined our trait data and calculated the variance in bolting time, flowering time, and flowering duration for each polyculture plot, and found little evidence for differences in synchronicity among natives and exotic polycultures (Table 2.4). Thus, it is possible that the complementarity we observed in both native and exotic polycultures may result from asynchronous growth.

Our relative fruit production results are more consistent with the work by Wilsey et al. (2009, 2011), showing that even though the exotics interacted complementarily with each other, they suppressed the relative fruit production of natives. If we examine just native-only polycultures, we see that native polycultures had 65% higher relative fruit production than native monocultures (mean relative fruit production in polycultures: 1.258 ± 0.090 s.e.m. *vs.* in monocultures: 0.762 ± 0.071 s.e.m.). This increase appears to be mostly due to positive trait-independent complementarity, but we also observed significant negative trait-dependent complementarity and dominance effects (Figure 2.2b) in the native polycultures. Thus, on average native species have higher fruit production in polyculture and native species with low relative fruit production in monoculture improved the most in polyculture. However, if we look at native performance in mixed-origin polycultures, we find that the presence of exotic species caused a 20% decline in native relative fruit production compared to that in native-only polycultures.

There are various mechanisms by which exotics might reduce the fruit production in natives, including competition (Levine et al. 2003), disruption of pollination services (Traveset & Richardson 2006), or increased susceptibility to herbivory (Rand & Louda 2004; Lau & Strauss 2005). We believe that competition from the exotics may be responsible for the suppression of fruit production in natives. When we account for changes in biomass in mixed polycultures (by dividing relative fruit production by plant biomass to get relative fruits/g), the previously significant interaction between plant origin and polyculture type (Figure 2.3) disappears ($F_{1,54}$ = 1.7, p = 0.1975), suggesting that exotics are suppressing native biomass and that this

Table 2.4 Mean variance in single-origin polycultures for phenological traits ± standard deviation. Variance was calculated within each plot, ln-transformed to improve the normality of the residuals and then analyzed with origin as the predictor variable. Native and exotic polycultures had equally variable bolting times ($F_{1,57}$ = 0.04, p = 0.843). Native polycultures had more variable flowering times ($F_{1,57}$ = 33.9, p < 0.0001) and exotics had more variable flowering durations ($F_{1,57}$ = 83.3, p < 0.0001).

Trait	**Exotic-only polycultures**	**Native-only polycultures**
time to bolt	181.7 ± 183.9	179.8 ± 247.6
time to flower	397.6 ± 254.5	916.5 ± 387.3
flower duration	948.4 ± 380.2	234.2 ± 187.8

suppression translates into reduced reproduction. Reduction in fruit production could have serious consequences over the long-term if recruitment of natives is seed-limited. For example, a multi-decadal examination of successional dynamics found that native species richness in invaded communities declined because the exotic species reduced the colonization rates of natives (Yurkonis et al. 2005) and seed limitation would exacerbate this problem. Interestingly, if we had examined only the biomass data or the fruit data, we would have drawn different conclusions about the effect of exotic plants on native diversity, which again highlights the importance of incorporating fitness measures into biodiversity experiments (Johnson et al. 2006; Parker et al. 2010).

Our choice of experimental study system may explain why, counter to predictions, exotic communities responded more positively to the diversity manipulation than did the natives, which presumably had more time to co-evolve. Fields were not common in the northeastern USA (where this experiment was conducted) before humans cleared the forest for agriculture and settlement (Cronon 1983). Historically, the species that now flourish in old-field communities probably grew in marginal habitats where forest cover did not established or in forest openings following tree-downs or fire (Marks 1983). If the disturbed and highly productive old-field habitat in which these species now grow and interact does not resemble the communities in which these species evolved, then perhaps we cannot expect stronger niche complementarity amongst the natives than amongst the exotics. Additional comparisons of native and exotic diversity in different habitats (with species that have

varying histories of interaction) and more precise measures of niche partitioning (Cardinale et al. 2011) would help to resolve this issue.

For arthropod communities, we also predicted that resource specialization (Hutchinson 1959; Murdoch et al. 1972; Strong et al. 1984) was more likely to operate in native communities, whereas resource-driven accumulation (Sriva stava & Lawton 1998) would apply in both native and exotic communities. Our results only partially support these predictions. Overall, we found that increasing native or exotic diversity resulted in a more abundant and diverse arthropod community. While arthropod abundance appears to be determined mostly by plant biomass, the mechanisms underlying richness are more complicated. The increase in arthropod richness in polycultures was not simply due to the presence of more arthropod individuals in polyculture (Srivastava & Lawton 1998), because rarefied richness (Gotelli & Colwell 2001) was significantly higher in both native and exotic polycultures compared to their respective monocultures. This suggests that resource specialization may be operating and that diverse plant communities recruited a greater diversity of arthropods because they offered a greater diversity of resources (Hutchinson 1959; Murdoch et al. 1972; Strong et al. 1984). The rarefaction analysis also showed that native monocultures and polycultures recruited more arthropod species (per arthropod individual) than did exotic communities. To our knowledge, we present the first comparison of how changes in native and exotic diversity impact arthropod community structure. However, other studies, which have compared arthropod communities on individual native and exotic species, have often found reduced faunal diversity on exotics (e.g., Agrawal et al. 2005; Burghardt et al. 2010). These results

combine to suggest that even though increasing the diversity of exotic species may enhance arthropod richness and abundance, equivalently diverse native plant communities may be better able to recruit a diverse fauna.

It is remarkable given the growing preponderance of exotic species in our landscapes (Sala et al. 2000) and the general trend that richness is increasing overall due to the inclusion of exotic species (Marks 2008; Sax et al. 2002; Ellis et al. 2012) that so few biodiversity experiments have independently manipulated native and exotic diversity to examine their effects on ecosystem and community functions (Wilsey et al. 2009; Wilsey et al. 2011). Our work, as well as that of others, suggests that exotic species can have positive effects on ecosystems (Davis et al. 2011; Jahner et al. 2011; Mascaro et al. in press), but our analyses of fruit production and arthropod community structure suggest that long-term negative effects may counterbalance these positive effects.

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CHAPTER 3

A DIRECT COMPARISON OF THE CONSEQUENCES OF PLANT GENOTYPIC AND SPECIES DIVERSITY ON ARTHROPOD COMMUNITIES AND ECOSYSTEM FUNCTION

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ABSTRACT

Biodiversity loss is proceeding at an unprecedented rate, yet we lack a thorough understanding of the consequences of losing diversity at different scales. While species diversity is known to impact community and ecosystem processes, genotypic diversity is assumed to have relatively smaller effects. Nonetheless, a few recent studies suggest that genotypic diversity may have quantitatively similar ecological consequences compared to species diversity. Here, we show that increasing either genotypic diversity of common evening primrose (*Oenothera biennis*) or species diversity of old-field plant species resulted in nearly equivalent increases (≈17%) in aboveground primary production. The predominant mechanism explaining this effect – niche complementarity – was similar for each type of diversity. Arthropod species richness also increased with both types of plant diversity, but the mechanisms leading to this effect differed: abundance-driven accumulation of arthropod species was important in plant genotypic polycultures, whereas resource specialization was important in plant species polycultures. Thus, similar increases in primary productivity differentially impacted higher trophic levels in response to each type of plant diversity. These results highlight important ecological similarities and differences between genotypic and species diversity, and suggest that genotypic diversity may play a larger role in community and ecosystem processes than previously realized.

INTRODUCTION

Rapid human alterations of the environment are leading to substantial reductions in biodiversity (Pimm et al. 1995, Chapin et al. 2000). These changes may have profound consequences, as diverse systems can be more productive (Tilman et al. 1996, Cardinale et al. 2007), stable (Reusch et al. 2005, Tilman et al. 2006) and resistant to invasions (Levine 2000) than less diverse systems. While most biodiversity research has focused on species diversity, recent work has found that genotypic diversity within species can also have pronounced ecological consequences (Wimp et al. 2004, Hughes et al. 2008, Parker et al. 2010). However, to date, there has been no direct comparison of either the relative importance of genotypic and species diversity, or the mechanisms by which genotypic and species diversity alter community structure and ecosystem functioning.

Greater productivity in diverse mixtures may be due to the increased probability of including a highly productive species (*i.e.,* the sampling effect), dominance of highly productive species in polycultures (*i.e.,* a positive selection effect), or reduced competition in polycultures due to niche partitioning or facilitation among the interacting species (*i.e*., positive complementarity) (Loreau and Hector 2001, Hooper et al. 2005). Niche partitioning, in particular, should be affected by trait variation and relatedness among interacting organisms (Petchey et al. 2004, Villeger et al. 2008, Cadotte et al. 2009, Hillebrand and Matthiessen 2009). Plant assemblages with greater trait variation are predicted to exhibit less niche overlap, more efficiently utilize resources, and achieve higher productivity than less variable assemblages (Cadotte et al. 2009, Hillebrand and Matthiessen 2009). Because trait variation within a single species is expected to be lower than trait variation among multiple species, one would predict that biomass increases in response to plant genotypic diversity

would be less pronounced than that of species diversity. Despite these expectations, a few recent studies have suggested that plant genotypic diversity may have similar impacts to species diversity on biomass, fitness, and other ecosystem functions (Schweitzer et al. 2005, Crutsinger et al. 2006, Johnson et al. 2006). However, these studies did not manipulate plant genotypic and species diversity simultaneously.

Two alternative hypotheses predict how general patterns of arthropod community diversity will respond to plant diversity (for hypotheses addressing responses of specific trophic levels, see Root 1973, Barbosa et al. 2009). The *resource specialization hypothesis* posits that because many arthropods specialize on distinct host plant species, increasing the number of plant species in a patch will attract a more diverse fauna (Hutchinson 1959, Strong et al. 1984). Alternatively, the *more individuals hypothesis* suggests that as available energy (*e.g.,* plant biomass) increases, there will be a greater number of arthropod individuals present, and thus a higher probability of observing more arthropod species (Srivastava and Lawton 1998). Because plant biomass is expected to increase with plant diversity, arthropod diversity is expected to also increase through abundance-driven accumulation of species. When considered in the context of plant trait variation, both of these hypotheses predict that the response of arthropods to plant species diversity will be greater than to plant genotypic diversity. In contrast, two recent studies have suggested that plant genotypic and species diversity may similarly impact the structure of higher trophic level communities (Crutsinger et al. 2006, Johnson et al. 2006).

In this study, we present the first direct comparison of the effects of plant genotypic and species diversity on arthropod species diversity and plant productivity (an ecosystem function) by simultaneously manipulating these two levels of diversity within a single field experiment.

MATERIALS AND METHODS

Study species and plant propagation

We manipulated plant genotypic diversity with *Oenothera biennis* L (Common Evening Primrose, Onagraceae), a native herbaceous plant that is common to old-fields and disturbed areas in eastern North America. *O. biennis* reproduces via a permanent translocation heterozygosity mating system, which results in clonally-related seeds (Cleland 1972) (i.e., all seeds produced by an individual plant are genetically identical to each other and the parent). *O. biennis* genotypes vary from an annual to perennial life-history strategy that is known to plastically respond to environment (Johnson 2007).

We collected *O. biennis* seeds from individual plants in 24 distinct populations around Ithaca, NY. Each genotype used in this experiment was determined to be unique using nine polymorphic microsatellite loci specifically developed for *O. biennis* (Larson et al. 2008). To reduce maternal effects, we first grew the seeds in a common garden in 2007, which was sprayed with insecticide at regular intervals throughout the growing season, and we used seeds collected from these plants (24 genotypes) for our experiment.

We focus on comparing the effects of plant genotypic versus species richness exclusively (and not functional group diversity) because genotypic variation within a species presumably offers no functional group diversity. Thus, for the species treatments we did not have nitrogen-fixers in the species pool, because the presence of this functional group can overwhelm effects of richness (Hooper et al. 2005, Cadotte et al. 2009). We used 24 species that are common in old-fields, co-occur with *O. biennis*, germinate easily, and do not possess particularly notable functional attributes: *Carex* sp.1, *Carex* sp.2, *Cichorium intybus*, *Daucus carota*, *Dianthus armeria,*

Dipsacus sativus, Elymus repens, Epilobium parviflorum, Galium mollugo, Leucanthemum vulgare, Pastinaca sativa, Penstemon digitalis, Phleum pratense, Plantago lanceolata, Rudbeckia hirta, Rumex crispus, Saponaria officinalis, Silene vulgaris, Solidago altissima, Symphyotrichum simplex, Symphyotrichum lateriflorum, Verbascum blattaria, Verbascum thapsus, and *Verbena hastata*. Seeds were collected from multiple individuals at three separate fields around Ithaca, NY in 2007 and pooled to generate genetically-diverse seed sources for each species. This species pool includes three annuals, six biennials, and fifteen perennials (Table 3.1).

We cold stratified (4°C, four days) all seeds in April 2007, sowed them into 96-well trays filled with soil (Pro-mix "BX" with biofungicide, Premier), and thinned germinated seedlings to a single individual per well. Plants were watered ad libitum and fertilized weekly (21-5-20 NPK, 150 ppm) while in the greenhouse (14:10 hour light:dark cycle, 5 weeks) and then field-hardened in an outdoor mesh cage (one substitutive design and our pools of 24 *O. biennis* genotypes and 24 old-field species, week) prior to planting in the field.

In late May 2008, we established the experiment in an abandoned agricultural field near Ithaca, NY where the soil was plowed, but otherwise untreated. Using a substitutive design and our pools of 24 *O. biennis* genotypes and 24 old-field species, week) prior to planting in the field.

Field establishment

We constructed four treatments: genotypic monocultures ("GM", one *O. biennis* genotype), genotypic polycultures ("GP", eight *O. biennis* genotypes), species

Table 3.1 Information for species employed in this experiment. Life history information is denoted as A = annuals, B = biennials, and P = perennials, and derives from the USDA Plants Database (http://plants.usda.gov). Biomass data is the average mass across the experiment per species (mean biomass per individual ± 1 s.e.m.)

Species	Family	Plant type	Life history	Biomass
*Oenothera biennis**	Onagraceae	Forb	AB	124.8 ± 2.8
Carex sp.1	Cyperaceae	Graminoid		5.2 ± 0.8
Carex sp.2	Cyperaceae	Graminoid		3.6 ± 0.5
Cichorium intybus	Asteraceae	Forb	BP	37.9 ± 6.3
Daucus carota	Apiaceae	Forb	AB	82.0 ± 8.6
Dianthus armeria	Caryophyllaceae	Forb	AB	9.5 ± 3.0
Dipsacus sativus	Dipsacaceae	Forb	AB	25.0 ± 2.4
Elymus repens	Poaceae	C3 grass	P	7.0 ± 0.7
Epilobium parviflorum	Onagraceae	Forb	P	27.5 ± 12.2
Galium mollugo	Rubiaceae	Forb	P	25.0 ± 1.9
Leucanthemum vulgare	Asteraceae	Forb	P	37.9 ± 3.7
Pastinaca sativa	Apiaceae	Forb	BP	22.8 ± 2.1
Penstemon digitalis	Scrophulariaceae	Forb	P	8.0 ± 1.7
Phleum pratense	Poaceae	C3 grass	P	11.1 ± 0.9
Plantago lanceolata	Plantaginaceae	Forb	ABP	46.1 ± 3.2
Rudbeckia hirta	Asteraceae	Forb	ABP	57.5 ± 5.1
Rumex crispus	Polygonaceae	Forb	P	21.7 ± 2.8
Saponaria officinalis	Caryophyllaceae	Forb	P	13.5 ± 1.6
Silene vulgaris	Caryophyllaceae	Forb	P	11.4 ± 1.5
Solidago altissima	Asteraceae	Forb	P	47.9 ± 4.9
Symphyotrichum simplex	Asteraceae	Forb	P	63.0 ± 7.0
Symphyotrichum lateriflorum	Asteraceae	Forb	P	7.1 ± 2.0
Verbascum blattaria	Scrophulariaceae	Forb	B	11.8 ± 2.5
Verbascum thapsus	Scrophulariaceae	Forb	B	3.8 ± 1.6
Verbena hastata	Verbenaceae	Forb	BP	50.1 ± 3.4

* 24 distinct genotypes of *Oenothera biennis* were employed in the genotypic diversity manipulation. Seeds for other species were genetically mixed for the species diversity manipulations.

monocultures ("SM", multiple genotypes of a single species that did not include *O. biennis*), and species polycultures ("SP", eight species that did not include *O. biennis*).

All plots contained eight equally spaced individuals arrayed in a ring 0.5 m in diameter. This density of plants is common in old-field plant communities and *O. biennis* populations (McArt and Cook, *pers. obs*.). The original design included 264 plots, but due to the loss of individuals within plots, we restricted our analyses to the 230 plots that experienced no mortality (GM: n = 46; GP: n = 69; SM: n = 66; and SP: n = 49). Every genotype or species appeared ~20 times in polyculture and 2-3 times in monoculture (except for two *O. biennis* genotypes that only had one monoculture each due to mortality and *Verbascum thapsus* which had no monocultures due to mortality).

In addition to the ring of plants, we grew a single *O. biennis* focal plant in the middle of every plot to test how the diversity treatments impacted natural selection on *O. biennis*. We ensured that the focal plant was always a different genotype than the *O. biennis* ring plants. Thus, our treatments are balanced such that species "monocultures" always contained two species (eight plants of the same species in a ring and one *O. biennis* focal plant) and genotype "monocultures" always contained two genotypes (eight plants of the same *O. biennis* genotype in a ring and one *O. biennis* focal plant of a different genotype), while polycultures always contained nine genotypes or nine species. The natural selection data will be presented elsewhere, but here we include the focal plant in analyses for completeness and accuracy (see Plant analyses).

Plots were separated by 1.5 m and we clipped encroaching weeds by hand every 2-3 weeks to ensure treatments remained consistent throughout the summer.

During the experiment 18 of the 24 species bolted and flowered, and all of the *O. biennis* genotypes bolted and flowered. For *O. biennis* genotypes and plant species that bolted, nearly every individual plant bolted and bolting did not vary by diversity treatments (O. biennis genotypes: Pearson $\chi 2 = 0.06$, $P = 0.80$; plant species: Pearson $\chi 2 = 0.39$, $P = 0.53$). Thus, diversity did not affect life-history expression of the plants.

Plant analyses

During the 2nd and 3rd week of October, we harvested the aboveground biomass of every plant, which was then dried (65°C) and weighed to the nearest 0.1g. We analyzed plant productivity via a two-way analysis of variance with main effects of diversity level (monocultures or polycultures) and level of plant relatedness (genotypic or species), plus their interaction (JMP, Version 7. SAS Institute Inc., Cary, NC, 2007). An alternative approach is to view this experiment as four distinct treatments and conduct analyses via a one-way ANOVA, which we have also done to verify that all two-way ANOVA results were similar to one-way ANOVA results. To account for spatial heterogeneity in the field, we divided the experiment into six blocks, where each block contained equal proportions of the four treatments, and included block as a random effect in all analyses. We analyzed both the full plot data (the sum of eight ring plants plus the focal plant) as well as the ring data alone (sum of the eight ring plants) for all of our analyses. Excluding the focal plant from our analyses (i.e., analyzing only the ring plants) did not alter the direction or significance of any of our results. We present the full plot data because it includes all the interactions that occurred in the plot.

Loreau and Hector (2001) devised a method to partition diversity effects into complementarity and selection effects. We modified this technique slightly to account for the absence of true monocultures (due to the focal plant in the middle of the ring). Whether a genotype occurred in the center or the ring had a substantial effect; for example, a single, representative genotype produced on average 110 g biomass in the ring versus 69 g as a focal plant. Thus, to determine the expected biomass of a ring plant in polyculture, we used the average value of an individual genotype or species from the monoculture ring. To determine the expected biomass of a focal plant, we took the average value of the 2 or 3 times that this genotype occurred in the middle of a genotypic monoculture (if calculating expected values for a genotypic polyculture) or a species monoculture (if calculating expected values for a species polyculture). Our modifications to Loreau and Hector's methods (2001) are indicated in bold, while the remainder of the text is replicated from the original paper.

Define for any polyculture:

- M_i **= average yield of an individual from species or genotype i in the low diversity treatment; for species this is the average of all individuals in a ring, for genotypes this was either the average of all individuals in a ring or of all individuals in the center of a genotypic or species monoculture**
- Y_{Oi} = observed yield of species i or **genotype i** in the polyculture
- $Y_O = \Sigma_i Y_{Oi} Y_O$ = total observed yield of the polyculture
- $RY_{Ei} = 1$ = expected relative yield of species i or genotype i in a polyculture (**which is 1 because the yield is expected to be identical to that in the monoculture**)

- $RY_{Oi} = Y_{Oi} / M_i$ = observed relative yield of species i or **genotype i** in the polyculture
- $Y_{Ei} = RY_{Ei}M_i = M_i$ = expected yield of an individual from species or genotype i in the polyculture
- $Y_E = \Sigma_i Y_{Ei}$ = total expected yield of the polyculture
- $\Delta Y = YO - Y_E$ = deviation from total expected yield in the polyculture
- $\Delta RY = RY_{Oi} - RY_{Ei}$ = deviation from expected relative yield of species i or **genotype i** in the polyculture
- N = number of species in the polyculture

Complementarity is calculated as $N\overline{\Delta RY}\,\overline{M_i}$ and selection as $N\text{cov}(\Delta RY, M_i)$. If we exclude the focal plant, the modification produces mathematically equivalent results to the original method and our results do not qualitatively change. Note that one species, *Verbascum thapsus*, did not survive in monoculture, so the three monocultures and ten species polycultures with this species were excluded from the complementarity and selection analyses.

To examine how competition intensity changed from monoculture to polyculture we calculated the corrected index of relative competition intensity (CRCI) (Oksanen et al. 2006). This index reduces bias inherent to other indices by extending the range of arguments where the function behaves linearly. To minimize errors due to the aberrant behavior of individuals, we first calculated mean values of individual genotype or species performance in each treatment. We then calculated competition intensity as (Oksanen et al. 2006) where Xr is the mean performance of a particular genotype or species in monoculture and Xc is the mean value in polyculture.

Arthropod analyses

In mid-July and again in mid-August, we censused arthropods by visually surveying every plant in the experiment (N = 2070 plants). We identified familiar arthropods in the field or collected specimens of unknown arthropods for later identification. To identify arthropods, we consulted relevant literature and the expertise of E. R. Hoebeke (Dept. of Entomology, Cornell University). Arthropods were identified to the lowest taxonomic level possible, generally species or genus and occasionally family. We also assigned arthropods to a feeding guild (herbivore, predator, omnivore or detritivore) based on relevant literature and the expertise of E. R. Hoebeke. We lumped together parasitoids that were less than 3mm in length (n = 10) because of logistical difficulties associated with their field identification. We did not attempt to count or identify arthropods that were less than 1 mm in length (*e.g.,* thrips, collembola).

Similar to the plant analyses, we used a two-way ANOVA with block as a random effect to test for the effects of plant diversity on cumulative arthropod abundance and richness. Repeated-measures analyses yielded qualitatively identical results to the cumulative dataset, so we chose the latter to facilitate more sophisticated follow-up analyses. We used a log+1 transformation on the abundance data to improve normality.

To test for the effect of plant biomass on arthropod abundance we divided arthropod abundance by the biomass of each plant and log-transformed the resulting data to improve normality. Division assumes a linear relationship between these two variables and indeed a linear function provided the best fit for the data (R^2 linear =

0.40, R^2 logarithmic =0.34). Next, because of the well known non-linear relationship between arthropod abundance and richness, we used individual-based rarefaction (Ecosim 7.0, (Gotelli and Entsminger 2006)) to test the effect of cumulative arthropod abundance on cumulative richness. We conducted rarefaction at each level of plant relatedness independently in order to compare arthropod communities drawn from the same distribution (Gotelli and Graves 1996). To test for differences in rarefied arthropod richness we used ANOVA with post-hoc independent contrasts.

We visualized the similarity among arthropod assemblages on genotypes and species with nonmetric multidimensional scaling (NMDS, Vegan 1.15-1, R version 2.8.1). The semimetric Bray-Curtis dissimilarity coefficient was used to compare arthropod assemblages on monocultures of O. biennis genotypes and plant species using a presence/absence dataset. We then conducted 500 simulations on a random dataset with identical parameters to verify that random stress (mean = 0.28) was significantly higher than model stress (mean = 0.23).

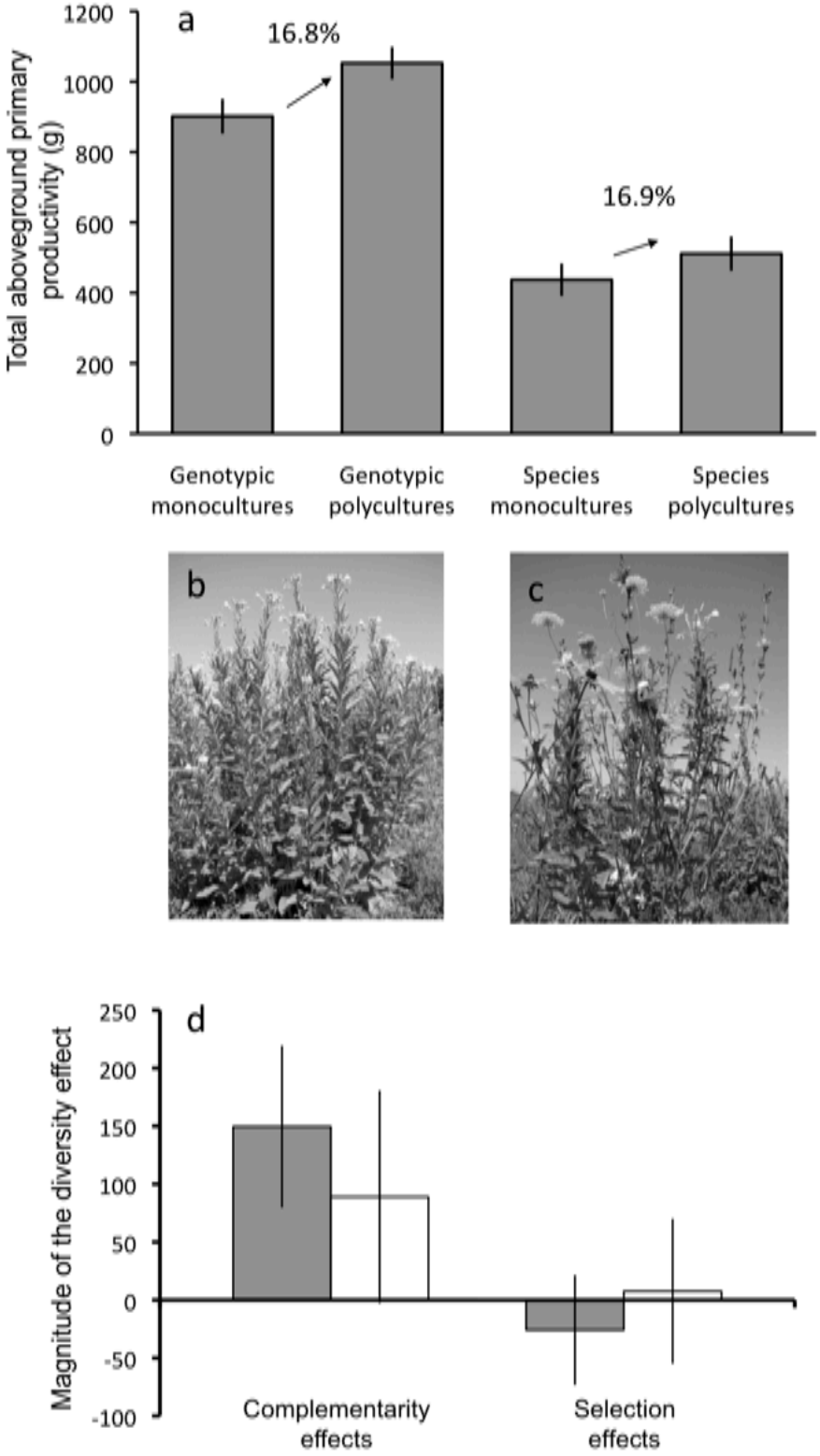
RESULTS

We found an overall positive effect of diversity on plot-level plant productivity (diversity: $F_{1,221.4} = 15.62$, $P = 0.0001$). Genotypic and species polycultures showed nearly equivalent increases in productivity (diversity × relatedness level: $F_{1,221.4} = 1.84$, $P = 0.18$): total biomass was 16.8% and 16.9% greater in genotypic and species polycultures than in monocultures, respectively (Figure 3.1a). Analysis via one-way ANOVA produced similar results ($F_{3,221.3} = 122.6$, $P < 0.0001$): post-hoc independent

contrasts on plant biomass indicated that genotypic polycultures were more productive than genotypic monocultures ($F_{1,221.4} = 14.0$, $P = 0.0002$) and that species polycultures were marginally more productive than species monocultures ($F_{1,221.1} = 3.4$, $P = 0.065$). While selection effects were weak to negative (Figure 3.1b), we found that complementarity among individuals contributed to the increases in plant productivity and did not differ between each level of relatedness ($F_{6,102}=1.06$, $P = 0.39$, Figure 3.1b). Another metric more commonly employed in the plant competition literature – the corrected index of relative competition intensity (CRCI) (Oksanen et al. 2006) – showed similar results: there were similar decreases in competition intensity with increasing plant diversity (-0.79 for genotypic diversity and -0.56 for species diversity, $F_{1,45} = 0.07$, $P = 0.79$). Thus, our comparable changes in complementarity and competition intensity may explain the remarkably similar increases in plot-level productivity that we observed in both genotypic and species polycultures of plants.

To determine the effects of plant biodiversity on higher trophic-level communities, we non-destructively surveyed arthropods that naturally recruited to each plant twice during peak growing season. In total, we made 76,753 observations of ~252 arthropod species. We found that arthropod richness increased with both types of plant diversity, but changed more dramatically in plant species polycultures (diversity × relatedness level: $F_{1,221.5} = 10.96$, $P = 0.001$; Figure 3.2a). Predators showed the most pronounced response to plant diversity, increasing in abundance 80% in species polycultures and 30% in genotypic polycultures (diversity: $F_{1,221} = 18.62$, $P < 0.0001$; diversity × relatedness level: $F_{1,221.6} = 4.42$, $P = 0.037$, Table 3.2), while increasing in richness 54% and 17% respectively (diversity: $F_{1,221.3} = 17.92$, $P <$

Figure 3.1 Plant diversity effects on productivity: (a) Genotypic and species polycultures had ~17% more biomass than their respective monocultures (LS means ± s.e.); (b) Genotypic polyculture; (c) Species polyculture. (d) The overall diversity effect can be partitioned into *complementarity* or *selection effects* (Loreau and Hector 2001) for genotype polycultures (dark columns) and species polycultures (light columns).


a
16.8%
16.9%
Total aboveground primary productivity (g)
1200
1000
800
600
400
200
0
Genotypic monocultures
Genotypic polycultures
Species monocultures
Species polycultures
b
c
d
Magnitude of the diversity effect
250
200
150
100
50
0
-50
-100
Complementarity effects
Selection effects

0.0001; diversity × relatedness level: $F_{1,221.8}$ = 3.87, P = 0.051; Figure 3.2a). Herbivores increased in abundance 44% and 30% in plant species and genotypic polycultures (diversity: $F_{1,221}$ = 8.54, P = 0.004; diversity × level of relatedness level: $F_{1,221.2}$ = 0.007, P = 0.93, Table 3.1), while increasing in richness 30% and 10%, respectively (diversity: $F_{1,221.4}$ = 28.76, P < 0.0001; diversity × relatedness level: $F_{1,220.9}$ = 6.80, P = 0.010; Figure 3.2a). Omnivores and detritivores showed similar patterns of increases in abundance and richness at both levels of relatedness (Figure 3.2a, Table 3.2), although responses were not as pronounced. A one-way ANOVA approach to these analyses produced qualitatively identical results (not shown).

To further understand how plant diversity at each level of relatedness affected arthropod community structure, we first evaluated the influence of plant productivity on the number of arthropod individuals. After dividing arthropod abundance by plant biomass, the previously significant effect of plant diversity on arthropod abundance disappeared ($F_{1,221.6}$ = 0.19, P = 0.66). Thus, arthropod abundance at both levels of relatedness was largely controlled by plant productivity and not by plant diversity *per se*. We next used rarefaction to determine whether increases in arthropod species richness would be best explained by arthropod abundance (*more individuals hypothesis*) or by arthropod specialization on distinct host plants (*resource specialization hypothesis*). Contrary to expectations, rarefied richness decreased with plant genotypic diversity (post-hoc contrast: $F_{1,212}$ = 9.04, P = 0.003; Figure 3.2b). This decrease in genotypic polycultures derives from a non-additive increase in the abundance of a single dominant species, *Plagiognathus politus* (Miridae), resulting in a lower richness than expected for that insect abundance. Removing *P. politus* from

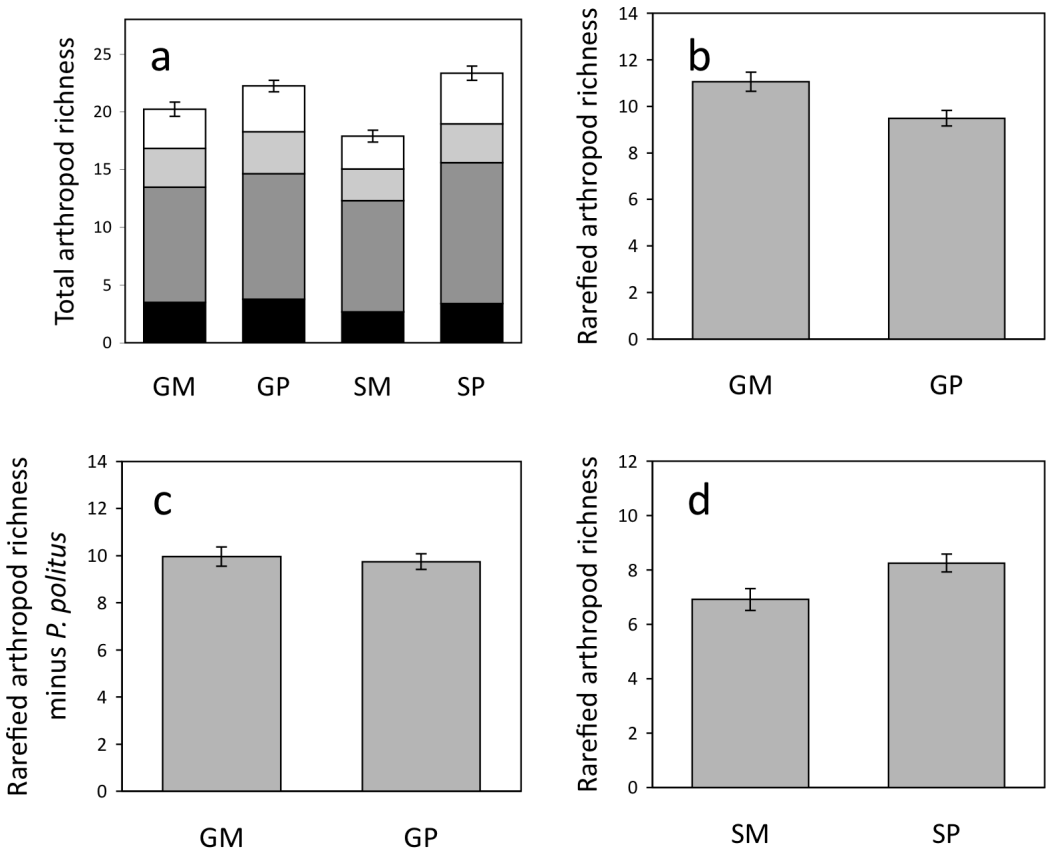


Figure 3.2 Relationship between plant diversity and arthropod richness: (a) Predators are represented in white, omnivores in light gray, herbivores in dark gray, and detritivores in black (Overall arthropod richness LS means ± s.e.); (b) Rarefied arthropod richness decreased with plant genotypic diversity (LS means ± s.e.); (c) After removing the dominant insect, *Plagiognathus politus*, from the dataset (*see* Results), rarefied arthropod richness showed no change with plant genotypic diversity (LS means ± s.e.); (d) Rarefied arthropod richness increased with plant species diversity (LS means ± s.e.); GM = genotypic monocultures, GP = genotypic polycultures, SM = species monocultures, SP = species polycultures.

Table 3.2 Responses of arthropod abundance and richness to plant genotypic and species diversity. Results summarize two-way ANOVA and post-hoc independent contrasts. Significant results ($P < 0.05$) are indicated in bold.

	Response	*Whole model*		*Plant species*		*Plant genotypes*	
		F	*P*	*F*	*P*	*F*	*P*
Diversity	**Abundance**	12.45	**0.001**	0.52	0.473	18.46	**<0.001**
	Predators	18.62	**<0.001**	19.67	**<0.001**	2.24	0.136
	Omnivores	8.40	**0.004**	0.02	0.898	18.12	**<0.001**
	Herbivores	8.54	**0.004**	3.87	**0.050**	4.96	**0.027**
	Detritivores	9.07	**0.003**	5.90	**0.016**	3.35	0.069
	Richness	44.86	**<0.001**	47.50	**<0.001**	6.57	**0.011**
	Predators	17.92	**<0.001**	18.62	**<0.001**	2.88	0.091
	Omnivores	11.75	**0.001**	11.03	**0.001**	2.31	0.130
	Herbivores	28.76	**<0.001**	29.67	**<0.001**	3.88	**0.050**
	Detritivores	6.38	**0.012**	6.17	**0.014**	1.17	0.280
Relatedness	**Abundance**	85.77	**<0.001**	22.44	**<0.001**	70.44	**<0.001**
	Predators	0.42	0.516	3.73	0.055	1.07	0.302
	Omnivores	86.89	**<0.001**	19.14	**<0.001**	78.26	**<0.001**
	Herbivores	36.04	**<0.001**	16.77	**<0.001**	19.35	**<0.001**
	Detritivores	5.73	**0.018**	3.96	0.048	1.94	0.165
	Richness	2.45	0.119	10.72	**0.001**	1.20	0.274
	Predators	0.26	0.608	2.81	0.095	0.95	0.332
	Omnivores	11.92	**0.001**	11.09	**0.001**	2.37	0.125
	Herbivores	1.18	0.278	0.97	0.326	6.51	**0.011**
	Detritivores	12.22	**0.001**	9.97	**0.002**	3.15	0.077
Diversity x Level of Relatedness	**Abundance**	6.30	**0.013**				
	Predators	4.42	**0.037**				
	Omnivores	9.53	**0.002**				
	Herbivores	0.01	0.930				
	Detritivores	0.19	0.659				
	Richness	10.96	**0.001**				
	Predators	3.87	0.051				
	Omnivores	1.68	0.197				
	Herbivores	6.80	**0.010**				
	Detritivores	1.01	0.315				

the dataset resulted in no difference in rarefied richness between treatments (Figure 3.2c). Both of these results are consistent with greater arthropod abundances causing higher arthropod species richness in genotypic polycultures, supporting the *more individuals* hypothesis. Conversely, rarefied richness increased with plant species diversity (post-hoc contrast: $F_{1,212} = 6.27$, $P = 0.01$; Figure 3.2d), indicating that the diversity of host-specific resources was important for the increase in arthropod richness. This result, in addition to the fact that the arthropod communities found on each plant species were far more divergent than the arthropod communities on each plant genotype (npMANOVA $F_{1,46} = 6.78$, $P < 0.0001$, Figure 3.3), highlights the importance of resource specialization for the arthropod community response to plant species polycultures.

DISCUSSION

We found that increasing either plant genotypic or species diversity led to quantitatively similar increases in primary production, and that the plausible mechanisms responsible for these effects – niche complementarity or decreased intensity of competition – were also similar for each type of diversity. A recent meta-analysis of the effects of biodiversity on primary productivity found that the most diverse species assemblages had on average 1.7 times more biomass than monocultures (Cardinale et al. 2007). However, effect sizes ranged dramatically, and nearly 21% of studies showed negative to no effect of increasing diversity (Cardinale et al. 2007). The limited genotypic diversity literature also reports a wide range of

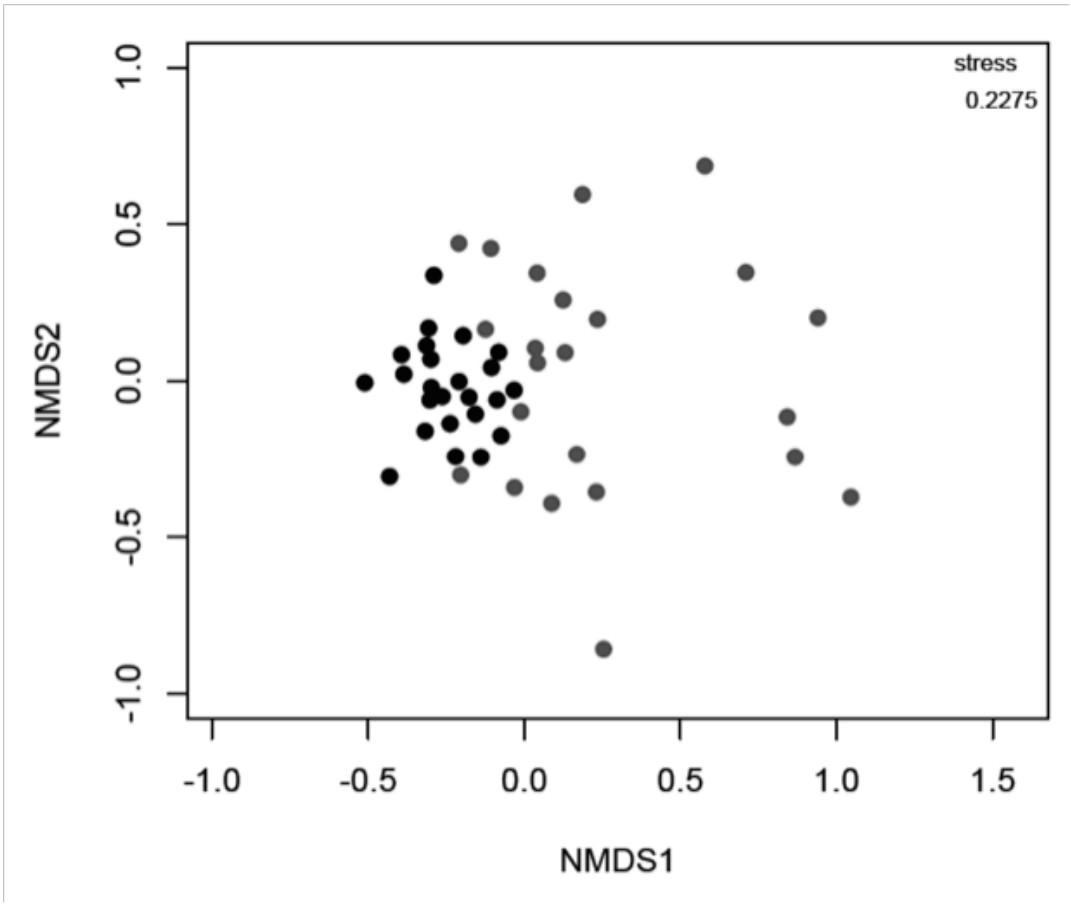


Figure 3.3 Nonmetric multidimensional scaling (NMDS) ordination of arthropod communities on each *O. biennis* genotype (black circles) and each old-field species (gray circles) obtained using two dimensions and 100 permutations. Each point represents the summed community of three monoculture plots of either an individual genotype or an individual species. Analysis of Bray-Curtis dissimilarity coefficients indicate that arthropod community assemblages are more dissimilar among species than among genotypes (npMANOVA: $R^2 = 0.13$, $F_{1,46} = 6.78$, $P < 0.0001$). 500 simulations on a random dataset with identical parameters were used to verify that random stress (mean = 0.28) was significantly higher than model stress (mean = 0.23).

increases in productivity across a diverse set of species: ~0 % in *Poa pratensis* (Vellend et al. 2010), ~14% in *Cakile edentula* (Dudley and File 2007), ~17% (Kotowska et al. 2010) and ~69% (Crawford and Whitney 2010) in *Arabidopsis thaliana*, ~36% in *Solidago altissima* (Crutsinger et al. 2006), ~39 % in *Lupinus angustifolius* (Milla et al. 2009), and ~58% in *Zostera marina* (Reusch et al. 2005); mean = 33%). Thus, the 17% increases in productivity that we observed at both levels of plant diversity were lower than average, but not atypical for genotypic or species diversity experiments. This variation among experiments, in addition to the comparison of vastly different experimental designs, highlights the importance of comparing the effects of genotypic and species diversity within a single field experiment, under similar conditions, and for the same duration of time.

Several factors may have contributed to the similar increases in plant productivity we observed with each type of diversity in this study. First, because the effect of species diversity on plant productivity generally increases with time (Cardinale et al. 2007), the similar effects of genotypic and species diversity that we observed may be a short-term phenomenon. Because plants comprising genotypic monocultures acquire resources very similarly, genotypic monocultures may become resource-limited more quickly than genotypic and/or species polycultures (where plants may overlap in their patterns of resource utilization, and thus utilize a larger pool of resources). Nonetheless, a recent study investigating the effects of genotypic diversity in *Solidago altissima* found that the effect of genotypic diversity on plant productivity over one growing season was similar to the effect of species diversity from a multi-year experiment (Crutsinger et al. 2006). Resource limitation is believed

to be a key mechanism of increased plant productivity in response to diversity (Hooper et al. 2005), and temporal variability in post-disturbance resource limitation along a continuum of plant genotypic to species diversity may be critical in predicting the effect size of increases in productivity. Understanding how trait variation and plant diversity interact temporally to affect ecosystem functioning represents an important gap in the literature, and we suggest that further studies are needed in this area of research.

A second important factor for our plant productivity results may be the specific species selected for this experiment. Genotypic diversity-productivity relationships have only been investigated in a handful of species (Reusch et al. 2005, Crutsinger et al. 2006, Dudley and File 2007, Milla et al. 2009, Bischoff et al. 2010, Crawford and Whitney 2010, Kotowska et al. 2010). Some of these species are particularly abundant in their communities (i.e., dominant species) and thus likely to grow at high intraspecific density – for example, goldenrods (Solidago *altissima*; Crutsinger et al. 2006) in old-field communities and eelgrass (*Zostera marina*; Reusch et al. 2005) in coastal estuaries. Frequent interactions with conspecifics may select for niche variation and thus increase the likelihood that the species will show a genotypic diversity-productivity effect. While *O. biennis* is not particularly dominant in old-field communities, it did respond very positively to the growing conditions at our field site, producing, on average, 3.8 times more biomass than the other species (Table 3.2). It is possible that larger plants are more likely to manifest a diversity effect, because they may more fully fill the available niche space, making nutrients limiting and accentuating the importance of niche partitioning. In addition, our species polycultures

did not include legumes, which have been shown to strongly contribute to effects of species diversity (Hooper et al. 2005, Cadotte et al. 2009). An ideal future experiment, though logistically large, might simultaneously manipulate genotypic diversity in multiple species with species diversity from a broader range of functional groups.

A third possible mechanism for the similar increases in plant productivity we observed in this study may be that higher trophic levels are dampening the response of species polycultures and/or amplifying the response of genotypic polycultures. For example, in a separate experiment with O. biennis, levels of arthropod herbivory were 26% higher in genotypic monocultures compared to polycultures (McArt, unpuplished data). If greater differences in herbivory occur between genotypic diversity treatments compared to those that occur between species diversity treatments, interactions with higher trophic levels may amplify the biomass increases observed with genotypic diversity. The contribution of herbivory to overyielding in plant diversity experiments has received some recent attention (*e.g.,* Haddad et al. 2009, Parker et al. 2010), but has yet to be compared among different types of plant diversity.

Lastly, non-linear declines in competition intensity with increasing genetic distance may explain the similar increases in plant productivity we observed in the genotypic and species diversity treatments. In other words, small changes in genetic distance among plants in genotypic monocultures versus genotypic polycultures may reduce competition to the same degree as much larger changes in genetic distance among plants in species monocultures versus species polycultures. Our data cannot distinguish among these multiple possibilities, yet each hypothesis is testable.

The second part of our study links arthropod community responses to each type of plant diversity. As expected, arthropod species richness responded less to plant genotypic diversity than species diversity (Figure 3.2a). Interestingly, divergent mechanisms led to the increases in arthropod richness with each type of plant diversity (Figure 3.2b-d, 3.3). Our data support the hypothesis that resource specialization influenced the arthropod response to plant species diversity while abundance-driven accumulation of species (more individuals hypothesis) influenced the arthropod response to plant genotypic diversity. These patterns fit the notion that insects are more likely to specialize on host plant species than host plant genotypes. However, resource specialization may be an important driver of arthropod responses to plant species hybrids and their backcrossed progeny (Dungey et al. 2000, Wimp et al. 2004, Evans et al. 2008) suggesting that comparing the similarity of arthropod communities (*e.g.,* Figure 3.3) across wider and more quantitative ranges of plant relatedness could greatly inform how plant genetics influences patterns of specialization and ultimately shapes arthropod community structure.

Overall, our results emphasize that diversity is inherently hierarchical and that within-species diversity can play a more important role in competitive interactions and community structure than previously realized. It is currently unclear whether the same factors causing declines in species diversity similarly impact genotypic diversity, or whether these two levels of biodiversity are causally connected (Vellend 2005, Lankau 2009). Nonetheless, variation within species is inevitably lost before species themselves go extinct (Vitousek et al. 1997). Considering our results in relation to the longstanding focus on plant species diversity and ecosystem functioning (Chapin et al.

2000, Reich et al. 2001, Hooper et al. 2005, Tilman et al. 2006), we suggest that more emphasis be placed on conserving variation within species, elucidating the ecological consequences of genotypic diversity, and discerning how diversity among traits, relatedness, and trophic levels interact.

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CHAPTER 4

POTENTIAL BENEFITS OF PLANT DIVERSITY ON VEGETATED ROOFS: A LITERATURE REVIEW

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ABSTRACT

Although vegetated green roofs can be difficult to establish and maintain, they are an increasingly popular method for mitigating the negative environmental impacts of urbanization. Most green roof development has focused on maximizing green roof performance by planting one or a few drought-tolerant species. We present an alternative approach, which recognizes green roofs as dynamic ecosystems and employs a diversity of species. We draw links between the ecological and green roof literature to generate testable predictions about how increasing plant diversity could improve short- and long-term green roof functioning. Although we found few papers that experimentally manipulated diversity on green roofs, those that did revealed ecological dynamics similar to those in more natural systems. However, there are many unresolved issues. To improve overall green roof performance, we should (1) elucidate the links among plant diversity, structural complexity, and green roof performance, (2) describe feedback mechanisms between plant and animal diversity on green roofs, (3) identify species with complementary traits, and (4) determine whether diverse green roof communities are more resilient to disturbance and environmental change than less diverse green roofs.

INTRODUCTION

By 2050 almost 9 billion people are predicted to inhabit the Earth and two-thirds of those are expected to live in urban areas (United Nations 2009). Urbanization triggers a suite of negative environmental impacts, including elevated pollution and

temperatures ("urban heat islands"), degraded streams and watersheds, and loss of native biodiversity (Grimm et al. 2008; Pickett et al. 2011). Incorporating diverse forms of vegetation into cities may help alleviate these problems by restoring ecosystem services (Bowler et al. 2010; Goddard et al. 2009; McKinney 2002).

Vegetated green roofs (Figure 4.1) integrate vegetation into underutilized urban spaces and are growing in popularity (Dunnett & Kingsbury 2004a; Oberndorfer et al. 2007). However, selecting appropriate plant species for green roofs remains a challenge because species must tolerate extreme temperature fluctuations, thin soils, and high winds (Dunnett & Kingsbury 2004a; Snodgrass & Snodgrass 2006). Tests of candidate species have focused primarily on identifying those that best tolerate rooftop conditions, resulting in a limited flora of a few drought-resistant *Sedum* species on many green roofs (Dunnett & Kingsbury 2004a; Snodgrass & Snodgrass 2006). Yet, by limiting the number and type of species in these systems, we may fail to treat green roofs as ecological communities and constrain the short- and long-term functioning of green roofs.

Although a strong positive link between plant biodiversity and ecosystem functioning has been well-established in the ecological literature (Hooper et al. 2005) and diverse green roof communities have been created (*e.g.,* Dewey et al. 2004; Dvorak 2003; Hauth & Liptan 2003; Köhler 2006), the empirical research linking plant biodiversity with green roof performance is limited. Thus, it is not surprising that green roof designers infrequently stray from *Sedum*-dominated planting schemes. Here, we combine the green roof and biodiversity-ecosystem functioning literatures to explore ecological dynamics on green roofs. We generate testable predictions about

how positive interactions among plant species may improve green roof performance, how diverse green roof plantings may support more abundant and diverse fauna, and how diverse green roofs may be less vulnerable to change. Finally, we conclude with a discussion of the types of species to test in diverse green roof communities. While other reviews have included abbreviated discussions of these topics (*e.g.,* Dvorak & Volder 2010; Francis and Lorimer 2011; Oberndorfer et al. 2007; Ranalli & Lundholm 2008) our review provides a more rigorous examination of the potential links between ecological biodiversity research and green roof design, and suggests an explicit research agenda for future green roof studies.

METHODS

We searched ISI Web of Science, Cornell University's library resources, and Google Scholar for relevant literature. Our search revealed five peer-reviewed articles in the green roof literature that explicitly manipulated plant diversity (Dunnett et al. 2008a; Kolb & Schwarz 1986; Lundholm et al. 2010; MacIvor et al. 2011; Nagase & Dunnett 2010). In contrast, there are hundreds of papers relating plant biodiversity to ecosystem function in the ecological literature, so we drew information from reviews and a subset of the relevant empirical work. Mostly, we used peer-reviewed articles, but include some papers from the annual Greening Rooftops for Sustainable Communities Conference when no relevant peer-reviewed articles existed.

POSITIVE INTERACTIONS AMONG PLANT SPECIES MAY IMPROVE GREEN ROOF PERFORMANCE

Plant species differ in how they utilize resources such as soil nutrients, water, and sunlight. Diverse communities composed of species with complementary resource use are expected to utilize total resources more completely and efficiently (Macarthur & Levins 1967; Tilman et al. 1996). This can lead to increased nutrient uptake, more efficient water usage and overall higher productivity (Darwin 1859; Hooper et al. 2005; Rixen & Mulder 2005; Tilman et al. 1996), and these effects may improve the ecosystem & provided by green roofs (Table 4.1).

PLANT PRODUCTIVITY, COOLING, INSULATION, AND RAINWATER RETENTION ON GREEN ROOFS

There is some evidence that diverse green roof communities are more productive than monocultures (Lundholm et al. 2010) and an increase in biomass may enhance multiple green roof services (Table 4.1). For example, Kolb and Schwarz (1986) found that temperatures below diverse green roof communities were cooler than below monocultures and suggested that the increased height and structural complexity (Figure 4.1) found in diverse mixtures formed air pockets that increased the roof insulation. Similarly, a large ecological experiment that manipulated plant species diversity in a field habitat found that temperatures in diverse plots were lower than in monocultures, although the cooling in this case was attributed to increased

Table 4.1 Green roof services and predicted impacts of increased plant species diversity. Citations marked with an asterix (*) are experiemental manipulations. Those marked with a cross (†) are from the green roof literature.

Services provided by green roofs	Predicted impact of diversity on green roof performance	Relevant citations
Temperature regulation (Bowler *et al.* 2010; Teemusk & Mander 2010) and mitigation of urban heat islands (Castleton *et al.* 2010) • Green roofs reflect more sunlight than conventional rooftops • Green roofs improve rooftop insulation • Rooftop plants cool the air via evapotranspiration. • Cooling and insulation reduce energy demands and costs	Increased plant productivity, structural complexity, and constancy of coverage will improve rooftop insulation Increased productivity and constancy of coverage will increase cooling via evapotranspiration and greater reflectance	Kolb & Schwarz (1986)*†; Del Barrio (1998)† Alexandri & Jones (2005)†; Kumar & Kaushik (2005)†; Verheyen et al. (2008)*; Lundholm et al. (2010)*†
Protection of watersheds due to absorbance and slow release of rainwater (Mentens *et al.* 2006; Czemiel Berndtsson 2010) • Vegetation slows rainwater runoff in urban areas, mitigating for high impervious surface coverage • Slowing runoff reduces demands on drainage networks	Increased complexity of vegetation will increase rainwater retention Increased plant productivity and constancy of coverage will increase evapotranspiration.	Rixen & Mulder (2005)*; Dunnett *et al* (2008a)*† Verheyen et al. (2008)*
Pollution uptake • from rainwater (Czemiel Berndtsson 2010) • from air (Getter & Rowe 2006; Yang *et al.* 2008)	Increased productivity, constancy of coverage will improve uptake of pollutants that can be used for plant growth (*e.g.*, CO_2, N and P) Differential nutrient use will increase nutrient pollution uptake (and reduce need for fertilizer)	Yang et al. 2008†; Pickett et al. (2011) Bracken (2006)*; Czemial Berndtsson (2010)†; Cardinale (2011)*
Mitigation for the loss of native biodiversity in urban environments (McKinney 2002) • create faunal habitat (Francis & Lorimer 2011)	Increases in productivity will increase arthropod abundance and richness Diverse green roofs will support more specialist species than less diverse green roofs Increasing diversity will improve the temporal stability of resources and better sustain dependent animal communities (*e.g.*, pollinators)	Brenneisen 2003†; Gedge & Kadas 2004†; Cook-Patton et al. (2011)* Colla et al. (2009)†; Gedge & Kadas 2004† Brenneisen 2004†; Menz et al. 2011
Enhancement of the aesthetic environment and overall human well-being (White & Gatersleben 2011).	Diversity will increase the aesthetic benefits of green roofs.	Fuller et al. (2007); Nagase & Dunnett (2010)*†;

evapotranspiration (Verheyen et al. 2008). Previous green roof research also linked higher biomass production to decreased water runoff, although the relationship between diversity and rainwater retention is ambiguous. Teemusk and Mander (2007) compared runoff on either side of a roof and found higher water retention on the side with denser vegetation (although they did not manipulate plant diversity). Dunnett et al. (2008a) manipulated plant diversity in green roof mesocosms, using a pool of four *Sedum* spp., four forbs and four grasses planted in monocultures, single functional group mixtures, or 12-*spp*. mixtures. The authors found a negative relationship between plant height and water runoff, but no clear relationship between plant diversity and rainwater retention. They hypothesized that structural complexity was more important than diversity. This merits further investigation because increasing plant diversity can increase structural diversity if functionally and morphologically different species are tested together (Spehn et al. 2000).

The above examples highlight the importance of distinguishing between biomass production and structural complexity. These three variables are likely frequently related, though not necessarily. Given that the amount of biomass suitable for green roofs is constrained by wind sheer, limited nutrient availability, load-bearing capacity, fire hazards, and ease of maintenance (Snodgrass & Snodgrass 2006), it may be important identify combinations of plants that optimize structural complexity rather than biomass *per se*.

Figure 4.1 Box of definitions of key terms and concepts

Green roofs are vegetated rooftops that consist of several layers including waterproofing, drainage, and insulation with soil substrate and actively growing plants on top (FLL 2008).

Intensive green roofs have soil substrates usually >15 cm deep and require more maintenance, whereas **extensive green roofs** have thinner soil and require less maintenance (Getter & Rowe 2006). Many more species, including small trees and shrubs, can survive on intensive roofs, but only small herbaceous species can survive on extensive roofs (Dunnett & Kingsbury 2004b, Dvorak & Volder 2010, Snodgrass & Snodgrass 2006).

Diversity is a general term that can be defined at multiple levels and encompasses variation within and among species. **Richness** refers to the number of species or genotypes present in an assemblage, but does not describe the differences among these units. **Functional group diversity** distinguishes species by broad morphological or physiological characteristics (*e.g.,* C3 grasses, C4 grasses, succulents, legumes, *etc.*) whereas **functional trait diversity** directly quantifies differences in trait means among species. Because it is often hard to know what traits are relevant and to measure them in all species, **phylogenetic diversity** can be measured instead of functional trait diversity. This metric quantifies relatedness among species, assuming that more distantly related species will have more variable traits, compete less, use the total resource pool more completely, and function better in diverse mixtures (Burns and Strauss 2011, Cavender-Bares and Wilczek 2003, Darwin 1859). Indeed, a recent meta-analysis showed that phylogenetic diversity was a better predictor of plant productivity than either species richness or functional group classifications (Cadotte *et al.* 2008).

Functional plant traits are traits that contribute to a green roof's ability to provide services to an urban area. Candidate functional traits for green roof plants are related to drought tolerance, phenology, and morphology (Dunnett & Kingsbury 2004b). Potential drought traits include mat or cushion growth forms, succulence, leaf trichomes (hairs) or waxes, a dormant life stage (*i.e.,* tubers) during harsh conditions, and low tissue maintenance costs during periods of low resource availability (Dunnett and Kingsbury 2004b, Eissenstat and Yanai 1997, Grime 2001). Dense trichomes reflect sunlight and increase the boundary layer around the leaf, helping to prevent water loss (Grime 2001). Also, increased endo- and exodermis layers in roots reduce water loss back to the environment (Enstone et al. 2002). Phenological traits are also important – annuals may work as an accent, but perennials improve the longevity of the planting (Snodgrass and Snodgrass 2006). Variation in flowering may help sustain animal communities (Dixon 2009; Menz et al. 2011).

Structural complexity has been implicated as important in roof insulation (Kolb 1986), rainwater retention (Dunnett et al. 2008a) and plant survival (Mulder et al. 2001), which suggests that variation in plant height, branching, and leafiness should also be considered when selecting green roof species.

COMPLEMENTARY RESOURCE USE AND POLLUTION UPTAKE ON GREEN ROOFS

Complementary resource use among species could also improve a green roof's ability to remove pollutants from air and rainwater (Table 4.1). A model of air pollution removal by green roofs found that on green roofs, tall herbaceous plants removed more ozone, NO_2, SO_2, and small particulates than short grasses (Yang et al. 2008). Thus, increases in biomass due to more efficient resource use could improve pollution removal on green roofs. In addition, species differ in how and when they absorb nutrients (Bracken & Stachowicz 2006), so diverse green roof communities could potentially absorb more nutrient pollution overall than an equally productive monoculture. Comparisons of prairie (Tilman et al. 1996), algal (Cardinale 2011), and seaweed (Bracken & Stachowicz 2006) communities report higher nitrogen uptake in diverse mixtures than in monocultures. The consistency of this pattern across multiple systems suggests that diverse green roofs may display similar ecological dynamics, but this prediction has not yet been tested. If nutrients are used more efficiently in diverse green roof communities, then a secondary benefit may be a reduced need for fertilizer on green roofs, which can itself be a source of nitrogen pollution in cities (Czemiel Berndtsson 2010; Oberndorfer et al. 2007).

Future research should examine how individual green roof species differ in pollutant uptake and how rates of pollution absorption change in diverse mixtures. Total uptake could be additive (Bracken & Stachowicz 2006) or non-additive (von Felten et al. 2009), depending on whether total absorption by a mixture can or cannot be predicted by each individual species' uptake. In addition, these examples discuss nitrogen pollution primarily, but green roofs have the potential to remove multiple pollutants from the air and water (Czemiel Berndtsson 2010; Yang et al. 2008) and we expect the effect of diversity to depend on pollutant type. For example, nitrogenous

compounds come in different chemical forms, so uptake is a function of what species are present and what form of nitrogen they prefer (Bracken & Stachowicz 2006), whereas carbon sequestration is more a function of plant biomass (Getter et al. 2009). Research into the individual and combined effects of green roof species on pollution uptake would help practitioners construct communities that optimize uptake of pollutants.

FACILITATIVE EFFECTS OF NEIGHBORING SPECIES ON GREEN ROOF PLANT SURVIVAL

Complementary resource use is relevant if plants are competing, but on some green roofs, especially extensive green roofs (Figure 4.1), abiotic stress may limit plant growth and survival more than competition (Snodgrass & Snodgrass 2006). In these harsh environments a plant can benefit from having diverse neighbors. For example, Mulder et al. (2001) manipulated bryophyte diversity in ecological mesocosms and found higher biomass production in diverse communities relative to monocultures, but only under drought conditions. The authors noted that the most drought-intolerant species in monoculture greatly benefited from growing in a mixture and suggested that the different architectures (*i.e.,* structural complexity) of the moss species increased the relative humidity and overall performance of diverse mixtures. Similar patterns have been observed on green roofs. Nagase and Dunnett (2010) experimentally manipulated water availability and plant richness on extensive green roofs, creating mesocosms from a pool of four *Sedum*, four forb, and four grass species. The authors compared plant survivorship in monocultures, single functional group mixtures, or 12-*spp*. mixtures and found higher plant survivorship in diverse communities under moderate aridity. Butler and Orians (2009) examined the growth of two herbaceous perennials (*Asclepias verticillata* and *Agastache rupestris*) in green

roof plots planted with and without *Sedum album* under different watering regimes. They found that *S. album* facilitated the growth of *A. rupestris* under drought conditions, but generally suppressed *A. verticillata* growth.

These studies suggest that species tested in monoculture (*e.g.*, Durhman et al. 2004; MacIvor & Lundholm 2011a; Wolf & Lundholm 2008) and deemed unsuitable for green roofs may actually perform well if planted with appropriate neighbors. Also, the exact identity (Butler & Orians 2009) and morphology (Mulder et al. 2001) of interacting species appears to be important, suggesting that increasing diversity alone may be insufficient. Future research should thus focus on establishing complementary species combinations to improve overall species survival.

DIVERSE GREEN ROOF PLANTINGS MAY SUPPORT MORE ABUNDANT AND DIVERSE FAUNA

Loss of native plant cover and diversity in cities has led to reductions in faunal richness, with native and non-native generalists replacing native specialists (McKinney 2002). However, green roofs could help maintain animal diversity in cities, since many animals naturally colonize green roofs (Dvorak & Volder 2010; Francis & Lorimer 2011), including spiders (Brenneisen 2003; Gedge & Kadas 2004), beetles (Brenneisen 2003; Hauth & Liptan 2003), soil invertebrates (Schrader & Böning 2006), bees (Colla et al. 2009; Tonietto et al. 2011), and birds (Brenneisen 2003; Fernandez-Canero & Gonzalez-Redondo 2010; Hauth & Liptan 2003).

Although some authors have hypothesized that plant structural diversity is an important determinant of faunal diversity (Brenneisen 2003; Gedge & Kadas 2004), there have been relatively few attempts to link green roof plant diversity with faunal diversity. MacIvor and Lundholm (2011b) measured arthropod diversity on green roofs and adjacent ground-level plots. When they included plant richness as a

covariate in the statistical model they found no effect of plant richness on arthropod diversity or abundance. In contrast, at least three other analyses found that green roofs with the highest plant diversity and/or structural complexity hosted the highest arthropod diversity (Brenneisen 2003; Brenneisen 2004; Gedge & Kadas 2004; Tonietto et al. 2011). In addition, many ecological experiments show a strong positive link between animal and plant diversity (Cook-Patton et al. 2011; Crutsinger et al. 2006; Haddad et al. 2009; Murdoch et al. 1972).

There are at least three potential reasons why increasing green roof diversity might enhance faunal diversity: (1) resource-driven accumulation of species, (2) resource specialization, and (3) temporal and structural diversity of resources (Table 4.1). Resource-driven accumulation of animal species occurs when increases in plant biomass increase the availability of food and nesting resources for animal communities on diverse green roofs. As resources increase, there will be more animals present, and thus a higher probability of observing more animal species (Srivastava and Lawton 1998). This resource-driven accumulation of species is probably more important on intensive green roofs, because the thinner soils on extensive green roofs limit plant productivity (Dunnett & Kingsbury 2004a).

Resource specialization occurs when some animals prefer only one or a few plant species as food or habitat (Hutchinson 1959; Strong et al. 1984). Thus adding more plant species to a green roof could attract more of these specialists. Specialist populations are generally declining as a result of habitat modification (Clavel et al. 2011) and are less common in urban areas (Devictor et al. 2007; Sorace & Gustin 2009). Planting both intensive and extensive green roofs with a diversity of plant species could potentially reverse these trends and help to attract and retain specialists in urban environments. For example, oligolectic bees collect pollen from a single family or genus of plant species and are therefore rare in urban areas unless their host

plants are present (Fetridge et al. 2008). To enhance specialist faunal diversity on a green roof, one might include plants from the Asteraceae family to attract *Melissodes* bees, plants from the Onagraceae family to attract *Lasioglossum oenotherae* bees, as well as plants important for other specialist bee species (Fetridge et al. 2008).

Lastly, greater plant diversity results in greater structural and resource complexity, which some species require for persistence (Goddard et al. 2009; Root 1973). This is especially true for natural enemies (predators and parasitoids), which require different prey and food resources, nesting sites and shelters (Landis et al. 2000; Root 1973). Many animals also require continuous resources throughout the season. For example, a bumblebee will perform better in a diverse plant community with species that flower at different times, because that community provides more stable nectar and pollen resources (Menz et al. 2011). Structural and resource complexity could occur at the level of a single rooftop or it could occur across a broader landscape. Given enough connectivity, green roofs within a city could act as a metacommunity (Leibold et al. 2004), with different rooftops providing different resources for urban-dwelling animals (Francis & Lorimer 2011; Goddard et al. 2009; Oberndorfer et al. 2007).

Research to determine which mechanisms (resource-driven accumulation of species, resource specialization, or resource diversity) are important under different conditions will help practitioners optimize the ability of green roofs to support animal biodiversity. For example, if resource-driven accumulation of species is found to be most important, then overall biomass would be more directly important than species diversity *per se* and intensive green roofs would be better at supporting faunal diversity than extensive roofs.

INCREASING DIVERSITY TO IMPROVE LONG-TERM GREEN ROOF PERFORMANCE

Green roofs are designed to provide multiple services (Table 4.1). The ecological literature suggests that diverse green roof plantings facilitate the long-term delivery of those services, because diverse communities may reduce the plant community's susceptibility to environmental change, pests, and invasion by weeds (Keesing et al. 2006; Levine et al. 2004; Root 1973; Yachi & Loreau 1999).

DIVERSE GREEN ROOFS MAY BETTER MAINTAIN FUNCTION DESPITE ENVIRONMENTAL FLUCTUATIONS

Yearly fluctuations in the environment can result in the mortality of sensitive species or genotypes. However, if there are multiple species/genotypes in a community, then other tolerant community members can grow and maintain coverage (Yachi & Loreau 1999). Seasonal fluctuations can also be important. If constant cover improves green roof function and aesthetics, then increasing diversity could help compensate for species that are temporally dormant (Getter & Rowe 2006).

However, there are few long-term analyses of how plant diversity changes through time on green roofs. Rowe et al. (2012) planted 25 Crassulaceaen species in three different media depths (2.5 cm, 5.0 cm, and 7.5 cm) and followed plant survival over multiple years. After two years about half of the species persisted in the 7.5 cm media depth and after five years only seven remained. Köhler (2006) examined plant diversity on an extensive green roof in Berlin during a 20-year period and found 110 plant species in total, but only a fraction of those species (10-15) were present consistently through time. Köhler noted that dieback was quite common, especially during dry years, but that annual plants often filled the gaps during wet periods and that wet summer months tended to increase plant diversity overall. Based on data

collected in a six-year survey, Dunnett et al. (2008b) noted that some species which appeared to thrive initially (*Sedum acre* and *Dianthus deltoides*) later showed declines, and were replaced by species that were previously less productive. All of these examples suggest that species determined to be appropriate at one time point, under one set of environmental conditions, may not persist in the long-term.

It is unrealistic to expect green roofs planted with few species to provide continuous cover with ever-fluctuating environmental conditions (Oberndorfer et al. 2007), especially considering that environmental stochasticity is expected to increase under climate change (Easterling 2000). Future research should identify groups of species that respond asynchronously to environmental conditions and/or complement each other temporally. Also, employing species that readily reestablish from a seed bank and/or resprout from rootstock would increase the species persistence through time and improve the community's ability to respond to fluctuations in the environment (Köhler 2006, Köhler & Poll 2010).

DIVERSE GREEN ROOFS MAY BETTER RESIST HERBIVORY AND DISEASE

Fluctuating weather conditions and seasonality are not the only factors impacting green roof stability; natural enemies like herbivores and disease organisms may also play important roles. The resource concentration hypothesis (Root 1973) predicts that specialist herbivore outbreaks will be more frequent in monocultures because high resource concentrations allow herbivore populations to grow to epidemic levels. However, we could find no peer-reviewed investigations of herbivory on green roofs, except a note that *Sedum spurium* produced low cover in one experiment because of a severe aphid infestation (MacIvor & Lundholm 2011a).

Disease incidence can also be lower in diverse systems (Elton 1958, Schnitzer et al. 2011). The dilution effect, one potential mechanism behind lower disease incidences, occurs when the presence of non-host species decreases disease transmission because propagules that hit non-hosts fail to propagate (Keesing et al. 2006). Even increasing genetic diversity within a species might help increase the long-term functioning of a green roof, as genotypes can vary in their susceptibility to a given pathogen (Power 1991). Because green roof plants are often stressed by abiotic factors, they may be quite susceptible to disease (Dunnett & Kingsbury 2004a). However, we were unable to find any experiments investigating disease prevalence or transmission on green roofs. Investigations into the frequency and severity of pest attack, as well as relationship between plant diversity and pest damage are thus needed to establish whether pests threaten green roof performance and if so, whether plant diversity improves a green roof's resistance and resilience to damage.

DIVERSE GREEN ROOF COMMUNITIES MAY BETTER RESIST INVASION BY UNDESIRABLE WEED SPECIES

Weed species may impair the aesthetics and/or long-term stability of green roofs. There are at least two testable mechanisms by which diverse green roof communities could resist invasion by weeds. First, disturbance often facilitates invasions by opening up resource space (Levine et al. 2004; Mack et al. 2000). If diverse communities are better able to maintain constant coverage through time, then we might expect fewer undesirable weed species to accumulate on green roofs with diverse flora than on species-poor roofs. Second, because species occupy different niches, diverse communities may better fill the available niche space and prevent intrusion by weeds (Funk et al. 2008; Zavaleta et al. 2004). Ecological experiments

have shown that diverse communities better resist invasions (Levine 2000), especially if the native community is phylogenetically-diverse (Gerhold et al. 2011; Figure 4.1). Thus invasions on green roofs may be best prevented by employing phylogenetically-diverse species assemblages, but this has yet to be established empirically.

TYPES OF PLANTS TO INCLUDE IN A DIVERSE GREEN ROOF COMMUNITY

There are multiple ways to quantify diversity (*i.e.,* species richness *vs* functional trait diversity; Figure 4.1) and the type of diversity that is best suited for a particular green roof habitat is currently not known. Increasing species richness (*i.e.*, the number of species present) may be insufficient. For example, with almost 600 *Sedum* species, it is quite possible to establish a species-rich green roof with only members of this genus (Snodgrass & Snodgrass 2006), but it is debatable whether a *Sedum*-only community optimizes green roof performance. To increase variation among community members, one might instead select species from different functional groups (e.g., succulents, C3 grasses, C4 grasses, legumes). The assumption underlying this functional group diversity approach (Figure 4.1) is that species from different functional groups have different morphological and physiological traits, and that variation in these traits allows species to interact more complementarily (Hooper et al. 2005). This is the type of diversity that has been manipulated in the few experimental examinations of diversity on green roofs (Dunnett et al. 2008a, Lundholm et al. 2010, Nagase & Dunnett 2010). However, these broad classifications treat species within a group as equivalent when there may be important distinctions among them. For example, a comparison of wetland and dryland plants on green roofs found greater variation within groups than between groups (MacIvor et al. 2011). Instead of lumping species into broad categories it may be more fruitful to examine

what key functional plant traits (Figure 4.1) each species possesses (Chapin et al. 2000, Lavorel & Garnier 2002).

It is also not known whether diverse native communities are better than non-native communities. In Texas grasslands, experimental manipulations of native and non-native plant diversity find that natives may interact more complementarily with each other than do non-natives and that species richness was maintained more in native than in non-native communities (Wilsey et al. 2009). Thus, the long term persistence of diverse communities may be better supported by planting native assemblages. Research also suggests that natives are beneficial in urban environments because they are more likely to support native wildlife and replace vegetation destroyed by development, as well as less likely to become invasive (Dunnett & Kingsbury 2004a; Burghardt et al. 2010; McKinney 2002; Tallamy 2007). On the other hand, green roofs are evolutionarily novel habitats and plant species that are native to an area in which a green roof is installed may not perform well in these habitats (Dunnett & Kingsbury 2004a). For example, Monterusso et al. (2005) tested 18 native species and 9 non-native *Sedum* species individually on a non-irrigated rooftop. Over three years, all the non-native *Sedum* species maintained coverage, compared to only four native species. These results do not show definitively that natives or non-natives are superior, because they compare functionally different species (*i.e., Sedum* species versus wildflowers and grasses). An improved experimental design would pair natives and non-natives from within a genus and thus compare species that are quite similar (due to a shared evolutionary history) but that differ in geographic origin (Agrawal et al. 2005). If a native *Sedum* mixture outperformed a non-native *Sedum* mixture, that would suggest that natives are better adapted to the biotic and abiotic conditions in that region.

It may also be more fruitful to employ species from habitats with environmental conditions that are more similar to green roof conditions rather than species native to a geographic location (Lundholm & Richardson 2010). Dunnett and Kingsbury (2004b) suggest looking at shortgrass prairies, California grasslands, and the Palouse prairie of Idaho for potential green roof plants, because these communities contain low-growing and drought tolerant species. Lundholm (2006) additionally suggests using vegetation on cliff and scree slopes as template communities. If *Sedum* species are preferred, then it may be helpful to find other species with which *Sedums* naturally co-occur. In sum, species that are "pre-adapted" to green roof conditions may perform better than species from non-analogous environments (Lundholm and Richardson 2010).

Finally, research needs to establish which species compositions are most effective at optimizing different green roof services (Table 4.1), because species vary in their contributions to different functions (Hector & Bagchi 2007). If the goal is to optimize a single green roof function, for example albedo, then it makes sense to select the single species with the highest reflectance. Adding species with less reflectance to increase diversity would only reduce the albedo of the green roof. However, if optimization of multiple green roof functions is desired, then higher levels of diversity may be required (Zavaleta et al. 2010). Lundholm et al. (2010) used a 15-species pool containing creeping shrubs, creeping forbs, succulents, grasses and tall forbs to create monocultures and mixtures containing one, three or five functional groups. When the authors examined a single green roof function, they found that some monocultures were as good, if not better, than mixtures at performing that function. However, when roof cooling, water capture, evapotranspiration, biomass production and stability of roof cover were considered together, no single plant type was best at performing all of these functions. Instead, performance was optimized by a mixture of

functional groups. Given the multi-faceted problems in urban environments (Grimm et al. 2008; McKinney 2002; Pickett et al. 2011) and the many potential services that green roofs can provide (Table 4.1), it may be possible to improve a green roof's ability to provide multiple services simultaneously by increasing the diversity of green roof communities.

CONCLUDING REMARKS

The goal of this review was to generate testable predictions about how ecological interactions among plants, animals, and the abiotic environment will impact the ability of green roofs to provide services in urban environments (Table 4.1). Because ecological dynamics on green roofs are only just beginning to be explored, we drew heavily from the biodiversity-ecosystem functioning literature to predict how changes in green roof diversity would affect green roof performance. While we provide conclusions and specific research recommendations at the end of each section, three larger themes emerge from the review.

First, it is important to distinguish between a species' ability to survive on a green roof and its ability to provide valuable services. Green roof conditions are harsh and *Sedum* species may have the highest survival without some irrigation. However, a more diverse mixture of species is more likely to provide multiple, effective green roof services compared to a *Sedum* monoculture. It may be necessary to alter green roof designs to facilitate the existence of species that are less drought-tolerant but more beneficial. For example, irrigation during very dry periods would allow one to employ a more diversified plant community (Getter and Rowe 2006). The creation of microclimates that vary in sun exposure and soil depth could also help increase plant diversity on extensive green roofs (Köhler 2006). While more maintenance may be

required to create and sustain a diverse community, the improvements in green roof performance could offer a high return on the investment of time and money.

Second, it is important to strategically select species because increasing diversity simply to increase diversity may not improve function. For example, MacIvor et al. (2011) found that adding wetland plants to green roof mixtures tended to decrease performance and suggested that the addition of less appropriate plants diluted the benefits of increasing species diversity. Similarly, Lundholm et al. (2010) note that their intermediate diversity treatment optimized green roof performance more than the highest diversity treatment and suggested that they were adding suboptimal species. This suggests that diverse communities created from random draws will probably be less effective than communities composed of species deliberately chosen for their complementary functional traits (Figure 4.1). Researchers must establish how variation in key traits impact green roof services and then determine which species mixtures maximize that variation.

Third, it is important to test species both in monoculture and in mixture to determine species contributions under varying environments. For example, species with poor drought tolerance in monoculture may be successful in polyculture (Mulder et al. 2001) and species with low evapotranspiration may improve evapotranspiration rates overall by facilitating the persistence of other species under drought conditions (Nagase & Dunnett 2010). Also, MacIvor et al (2011) found that plant combinations containing the dryland grass *Danthonia spicata*, maximized water capture, even though *D. spicata* in monoculture captured very little water. All of these examples highlight how the performance of individual species (and their contribution to overall green roof function) may depend on the diversity of the surrounding community.

In conclusion, ecologically-informed green roof designs could optimize the role of green roofs in mitigating the loss of ecosystem services in urban areas.

Although the use of *Sedum* species has been viewed as a necessity because of the extreme abiotic conditions on green roofs, it is too soon to rule out diverse green roof communities when their potential benefits are so great.

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